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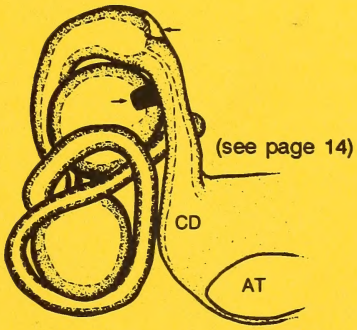

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THE SPERMATHECAL PORES OF SPIDERS WITH SPECIAL REFERENCE TO DICTYNOIDS AND AMAUROBIOIDS (ARANEAE, ARANEOMORPHAE, ARANEOCLADA)

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Abstract *Proc. ent. Soc. Ont.* 123:1-21

Two types of spermathecal pore structures occur in the vulvae of spiders. One or more simple "primary" pores of uncertain function are well known but not often discussed. Likely they are plesiomorphically present in all spiders. Complex "dictynoid" pores (probably an apomorphy of Dictynoidea) of unknown function are here described for the first time and their distribution in spiders is examined. The placement of primary and dictynoid pores is used to identify homologous regions among the vulvae of the taxa examined.

Introduction

The copulatory organs are the most important indicators for identifying spider species and can provide valuable characters for phylogeny reconstruction. Coddington (1990b) and Sierwald (1989, 1990) have lamented the lack of information about homologies among male palpal sclerites and female vulval components above the family level. Simple pores penetrating the spermathecae of spiders (Figs. 2, 5, 12, 18) are of very widespread occurrence and may be plesiomorphically present in all female spiders (Forster *et al.* 1987; Sierwald 1989). As such, and assuming they are homologous, these pores can serve as important markers of homologous regions in the spermathecae of diverse taxa.

In spite of their acknowledged widespread occurrence spermathecal pores have been virtually ignored as taxonomic characters. Among taxonomic and systematic works only those dealing with liphistiomorphs (e.g. Platnick and Sedgwick 1984), mygalomorphs (e.g. Coyle 1981; Goloboff and Platnick 1987; Griswold 1987), and the most primitive araneomorphs (palaeocribellates and austrochiloids: e.g. Forster *et al.* 1987) routinely discuss or at least illustrate spermathecal pores. Perhaps this is because the pores are prominent features of the relatively simple saccate spermathecae in these spiders. The vast majority of spider taxonomic and systematic literature deals with the "higher" araneomorphs (Araneoclada—haplogynes and entelegynes) in which the spermathecae are generally much more complex. In these works spermathecal pores are rarely mentioned or illustrated (even the most recent general spider biology text [Foelix 1982] gives them only meagre coverage). Only Sierwald (1989), in determining homologies amongst pisaurid spermathecae, appears to have recently addressed spermathecal pores.

Little is known of their function. Passage of secretions into the spermatheca is undeniable: many authors have demonstrated that glands envelope the pores and drain through them into the spermatheca (e.g. Petrunkevitch 1925; Opell 1979, 1983; Kovoor 1981; Coyle *et al.* 1983; Lopez and Juberthie-Jupeau 1983; Forster *et al.* 1987). Several hypotheses of function, not necessarily

mutually exclusive, have been proposed but remain unproven. These (briefly reviewed in Lopez 1987) include pheromone production (Kovoor 1981), sperm nutrition (Forster 1980; Coyle *et al.* 1983) and/or activation (Lopez and Juberthie-Jupeau 1983; references in Opell 1983), and mechanical displacement of sperm from the spermathecae into the fertilization ducts during fertilization (Forster *et al.* 1987; Lopez 1987).

Some spiders have two types of spermathecal pores: simple ones as discussed above as well as more complex ones (described below) usually located on the spermathecae near the fertilization ducts (Figs. 1, 4, 7, 12). Prior to this study these complex pores were unknown although Roth (1952: 213, 215, 218), in a study of *Cybaeus* L. Koch, briefly mentioned nonconformities on the surface of the spermathecae which are undoubtedly the complex pores. During the preparation of a revision of the Nearctic Cybaeidae (Bennett 1991) I studied the complex pores in depth. At first it seemed these pores could be an apomorphy defining Cybaeidae but it soon became apparent that they are more generally distributed. They may be synapomorphic for most, if not all, Dictynoidea *sensu* Forster (1970), a grouping encompassing the entelegyne families Dictynidae, Megadictynidae, Hahniidae, Desidae, Cybaeidae, Argyronetidae, and Anyphaenidae (including Amaurobioididae) (see Coddington [1989] for a discussion of the monophyly of Dictynoidea.) For this reason the simple spermathecal pores are here referred to as "primary" pores and the more complex ones as "dictynoid" pores.

Where spider vulval ontogeny has been examined in detail, the primary pores are evident at a very early stage (Bhatnagar and Rempel 1962; Sierwald 1989; Bennett 1991). Dictynoid pores, however, apparently develop only in the final stages (Bennett 1991).

Methods

The following entelegyne taxa were examined for the presence of dictynoid pores particularly, but also for primary pores. Vulvae with dictynoid pores are described in greater detail than those without.

Except for *Callioplus*, *Dictyna*, *Neoantistea*, *Phrurotimpus*, and *Hogna* these taxa are/were members of the polyphyletic Agelenidae *sensu lato* and were selected because of an underlying interest in the true relationships of the traditional agelenids, especially the cybaeids. Lehtinen's (1967) radical redefinition of the Agelenidae resulted in most of the familial placement recorded below. Modifications from Lehtinen's classification (e.g., coelotines in the Amaurobiidae) follow the catalogue of Platnick (1989). Both Brignoli (1983) and Platnick (1989) accepted the majority of Lehtinen's changes but expressed concerns (Lehtinen's taxonomic novelties are not based on definitive apomorphies—but see Griswold's [1990:13, 20] discussion of Lehtinen's concept of Agelenidae).

Amaurobioidea:

Agelenidae:	*Agelenopsis potteri* (Blackwall), *Tegenaria domestica* (Clerck).
Amaurobiidae:	*Callioplus macarius* Chamberlin, "*Coelotes*" sp., *Coras juvenilis* (Keyserling), *Rubrius antarcticus* (Karsch), *Wadotes calcaratus* (Keyserling).
Lycosidae:	*Hogna helluo* (Walckenaer).

Dictynoidea:

Argyronetidae:	*Argyroneta aquatica* (Clerck).

Dictynidae: *Blabomma californica* (Simon), *Cicurina bryantae* Exline, *C. intermedia* Chamberlin and Ivie, *Cicurina* sp., *Dictyna coloradensis* Chamberlin, *Yorima angelica* Roth.

Cybaeidae: *Cybaeus* spp., *Cybaeota shastae* Chamberlin and Ivie, *Cybaeozyga heterops* Chamberlin and Ivie

Hahniidae: *Calymmaria montavencis* (Bishop and Crosby), *Calymmaria* sp., *Cryphoeca exlineae* Roth, *Dirksia cinctipes* (Banks), *Ethobuella tuonops* Chamberlin and Ivie, *Neoantistea* sp., *Neocryphoeca beattyi* Roth, *N. gertschi* Roth.

Uncertain placement:

Liocranidae: *Phrurotimpus borealis* (Emerton).

In this paper Sierwald's (1989) terms for the components of the female spider's copulatory organs are followed in an effort to standardize names of presumably homologous parts in different taxa. Thus epigynum refers to the external components including the atrium or atria which is/are one or two cavities leading into the vulva. The vulva is comprised of the paired internal components: the copulatory ducts (joining the atrium/atria to the spermathecae), the spermathecae (in which sperm are stored and the pore structures are located), and the fertilization ducts (through which sperm pass from the spermathecae to the uterus externus during fertilization). Each spermatheca has a head (containing the primary pores), stalk (with usually one dictynoid pore if such pores are present), and base. In many taxa these divisions are not distinct and can only be determined by the presence of pores. See Bennett (1991) for a discussion of the homology of the female copulatory organ components in various spider taxa.

Specimens used in this study are in the author's collection unless otherwise stated. Vulvae were excised from spiders preserved in 75% ethanol, cleared in clove oil, and examined with a Leitz Laborlux compound microscope. Some were cleared with a commercial contact lens cleaner solution (Sierwald 1991), dehydrated in absolute ethanol, mounted on standard SEM stubs, and sputter coated with gold palladium prior to examination in an S-570 Hitachi scanning electron microscope.

Abbreviations used in figures are explained in the legends for Figures 1-14.

Results

Pore Structure and Placement

Primary pores are simple canals which convey gland ducts through the walls of the spermathecal heads. Histological sectioning and staining techniques are normally needed to demonstrate the glandular tissue associated with the primary pores but often in specimens cleared with clove oil or contact lens cleaner the gland ducts or remnants of them (Figs. 2, 32) appear as small, lightly sclerotized threads emanating from the pores. Primary pores are normally most easily observed in dorsal views of spermathecae. Their presence defines the spermathecal head. The heads are of highly variable form: membranous to heavily sclerotized (Figs. 1-3) and variously lobed and distinct (Figs. 4, 20, 33, 38, 42) to essentially indistinguishable (except for the primary pores) from the rest of the vulval ducting (Figs. 12, 18).

The dictynoid pores occur as a single, porous plate in the bottom of a shallow, circular concavity (Figs. 2, 6, 12, 21) located on the spermathecal stalk. In some cybaeid species the porous plate is everted (Bennett 1991, Figs. 454, 457, 544). In cleared specimens the pore plate

can be seen to traverse the wall of the spermathecal stalk (Figs. 10, 15, 17, 19) and often it appears to be more or less extended into the lumen of the stalk (Figs. 14, 22, 26). The spermathecal stalk serves to connect the head with the spermathecal base. As in the head, the stalk is of variable form: distinct and bulbous (Fig. 4) to slender and indistinguishable from the rest of the spermatheca (Bennett 1991, Figs. 511, 516, 530) to at least partially incorporated into the base (Figs. 10, 14, 19, 23). The stalk is normally well sclerotized.

Pore Distribution

All taxa examined have primary pores. Of the above *Tegenaria domestica*, *Rubrius antarcticus*, the cybaeids, dictynids (except for *Dictyna coloradensis*), hahniids (except for *Neocryphoeca gertschi*), and *Argyroneta aquatica* all (apparently) have *Cybaeus*-type dictynoid pores. *Agelenopsis potteri* and *Phrurotimpus alarius* have primary pores in two distinct groups, one comprising one or a few pores and the second with many. The lycosid and the amaurobiids (exclusive of *Rubrius*) have primary, but lack dictynoid, pores.

Taxa with dictynoid pores:

CYBAEIDAE: Bennett (1991) documented primary and dictynoid pores in all known Nearctic cybaeid species except for some species of *Cybaeota* which were not specifically examined for pores. For detailed descriptions of cybaeid vulvae see Bennett (1988, 1991). A few representatives are presented here.

1. *Cybaeus* spp. (Figs. 1-6). The species of this genus generally have distinct spermathecal heads, stalks, and bases with numerous small primary pores dorsally on the heads and a single, conspicuous dictynoid pore distally on each stalk close to the junction with the spermathecal base. In some species the dictynoid pore is incorporated into the spermathecal base (Bennett 1991, Figs. 421, 430).
2. *Cybaeota shastae* (Figs. 10-11). A few primary pores are located on an inconspicuous, membranous lobe near to the atrium (Fig. 11). Each spermathecal stalk is short and simple with the dictynoid pore incorporated into the wall of the spermathecal base (Fig. 10).
3. *Cybaeozyga heterops*, in AMNH. The copulatory apparatus of *C. heterops* was not drawn during this study. Its minute epigynum and vulva correspond closely to Roth and Brame's (1972, Fig. 25) drawing of uncleared genitalia. The single transverse atrium apparently opens laterally directly into each half of the vulva. Copulatory ducts are very short. Head, stalk, and base of each spermatheca are combined into a transversely oriented, oblong bulb. Each bulb bears medially on its anterior margin a dictynoid pore and on its anterior inner lateral margin one or, at most, a very few primary pores. Each bulb is antero-posteriorly divided internally into halves with the inner half bearing the primary pore(s) and the outer half the dictynoid pore.

DICTYNIDAE:

1. *Blabomma californica* (Fig. 12). This species of *Blabomma* has a single, transverse atrium medially on the epigynum with very short copulatory ducts broadly and shallowly joined across its anterior margin. The head of each spermatheca (with a small, dorsal group of primary pores) is very close to the atrium at the beginning of and continuous with a short, well sclerotized spermathecal stalk. The stalk leads into a large, thick-walled, bulbous base with a simple lumen and bearing a large, conspicuous dictynoid pore dorsally at the junction

of stalk and base. The fertilization duct exits the base posteriorly close to the entrance of the stalk.

2. *Cicurina bryantae* (Figs. 17-18). The genus *Cicurina* shows a wide range of genitalic form (see figures in Chamberlin and Ivie 1940). The female copulatory apparatus of *C. bryantae* is representative of the simplest form and is similar to that of *Blabomma californica*. Here the atrium is a single, transverse opening posteriorly located on the epigynum (Bennett 1985, Figs. 3, 5). The copulatory ducts are relatively large, broad, anteriorly directed and weakly joined at the midline of the vulva. The lumina of the copulatory ducts gradually narrow anteriorly and the ducts lead directly into the more heavily sclerotized spermathecal heads near the anterior margin of the vulva. Primary pores are found both dorsally and ventrally on the heads. The heads are continuous with the spermathecal stalks which extend to the anterior margin of the vulva then turn posteriorly to join ventrally with the spermathecal bases at the posterior margin of the vulva. The bases are oblong, bulbous, and have simple lumina. Each base has a single, large dictynoid pore on its inner lateral margin near the entrance of the stalk. The fertilization ducts exit the bases posteriorly.
3. *Cicurina intermedia* (Fig. 15), *Cicurina* sp. (Fig. 16). These two species are representative of those *Cicurina* with more complex vulvae. The former has a single, large, transverse, oval atrium with the copulatory ducts very shallowly joined across its anterior margin. The ducts are fairly narrow and lead to the anterior vulval margin. Here the lumen of each becomes very narrow for a short distance then broadens into the spermathecal head which bears a few primary pores dorsally. The spermathecal stalks are long, convoluted, simple ducts continuous with but of slightly narrower diameter than the heads. Distally each stalk is greatly expanded and bulbous and bears a large dictynoid pore as well as the fertilization duct. Posteriorly a narrow duct leads from this bulb into a second, blind one which is probably the spermathecal base. The unidentified species considered here differs in having a much smaller atrium, a larger region of joined copulatory ducts, slightly different placement of the primary pores, and longer spermathecal stalks.
4. *Yorima angelica* (Figs. 13-14), in MCZ. Here the atria are paired, comma-like depressions found near the midline of the epigynum. The vulva in this species is relatively simple. The copulatory ducts are short, anteriorly directed, and contiguous but with separate lumina. Unfortunately primary pores were not looked for and their presence cannot be confirmed. It is predicted, however, that they are at the anterior end of the vulva where the ducting turns posteriorly. The spermathecal stalks are short and straight and enter the bulbous bases dorsomedially. A large dictynoid pore is located on each base at the junction with the stalk. The lumina of the bases are relatively complex. Fertilization ducts exit the bases posteriorly.

AMAUROBIIDAE:

1. *Rubrius antarcticus* (Fig. 21), in AMNH. In this species the paired atria are widely separated at the posterolateral margins of the epigynum (Lehtinen 1967, Fig. 160; Roth 1967, pl. 52 Fig. 12). The copulatory ducts are long. They proceed towards the midline from the atria, then to the anterior epigynal margin, then reversing direction to the posterior margin before joining the spermathecae posterolaterally dorsal to the atria. The spermathecae are unipartite and bulbous with a small group of primary pores anteriorly and a large dictynoid pore posterodorsally between the entry of the copulatory duct and the exit of the fertilization duct. The lumina of the spermathecae are undivided.

AGELENIDAE:

1. *Tegenaria domestica* (Figs. 25-30). The atrium is single and posteriorly located on the epigynum in this species (Roth 1968, Fig. 16). The copulatory ducts are broadly and shallowly joined along the anterior margin of the atrium and lead into compact, unipartite, laterally located spermathecae. The lumina of the spermathecae are compartmentalized. Primary pores are on the outer lateral margin (one large, round pore) and medially (one or a few small pores) on each spermatheca. A large, bean-shaped dictynoid pore is situated near the inner lateral margin. The two large pores are here differentiated as primary and dictynoid pores on the basis of their internal structure as seen in cleared vulvae: the dictynoid pore appears to have a complex sieve plate structure while the primary pore is simple.

ARGYRONETIDAE:

1. *Argyroneta aquatica* (Figs. 7-9), in AMNH. This is another species with a very simple, compact vulva. The atria are paired and widely separated at the lateral margins of the epigynum (Roberts 1985, Fig. 68a). Short copulatory ducts open into compact, bulbous spermathecae. One or a few primary pores are located anterodorsally close to the inner lateral margin of each spermatheca and near to the entrance of the copulatory duct and exit of the fertilization duct. A single, large, anteriorly located dictynoid pore is near the primary pores but closer to the outer lateral margin of each spermatheca. The lumina of the spermathecae appear to be compartmentalized but the very thick walls of the spermathecae make this difficult to ascertain.

HAHNIIDAE:

1. *Calymmaria montavencis* (Fig. 20), *Calymmaria* sp. (Fig. 19). Both of these species have a single small atrium located anteriorly on the epigynum (Bishop and Crosby 1926, Fig. 53) and very short copulatory ducts. In *C. montavencis* the heads of the spermathecae are short lobes projecting anteriorly from the region of the atrium and bearing primary pores apically. The stalks in this species have thick walls, narrow lumina, and lead from the atrial region to the posterior margin of the vulva. There they turn anterolaterally and enter the large, bulbous spermathecal bases. A dictynoid pore is incorporated into the dorsolateral wall of each base at its junction with the stalk. The fertilization duct exits each base adjacent to the entry of the stalk. The unidentified species is very similar except that the atrium is the anteriormost component of the copulatory apparatus and the spermathecal heads are small dorsal vulval lobes located somewhat posterior of the atrium.
2. *Dirksia cinctipes* (Figs. 23-24, 31-32). This species has paired, longitudinal atria running along the midline of the vulva (Chamberlin and Ivie 1942, Fig. 37). Short, small, and separate copulatory ducts enter the spermathecae anteriorly. Each spermatheca is simple, bulbous, and possesses an interesting arrangement of pores. The dictynoid pore is located near the outer anterolateral margin opposite the entrance of the copulatory duct. The primary pores are in two groups: a single pore on a slight prominence just posterior to the dictynoid pore and, further posteriorly, a group of pores within a small pit. The lumina of the spermathecae are undivided and the fertilization ducts are small and inconspicuous posteriorly.
3. *Neoantistea* sp. (Fig. 22). Although Opell and Beatty (1976) recently revised the Nearctic hahniids this species cannot readily be placed in any of the described ones. It has the spiracle placement characteristic of *Neoantistea* but lacks the large bulbous spermathecal component (base ?) evident in most species (see figures in Opell and Beatty). The atria here are paired, small, inconspicuous, and anteriorly located on the epigynum. The copulatory ducts are very

short, leading immediately into the spermathecae. At the anterior end of each spermatheca is a small, lateral head with primary pores posteriorly. The rest of the spermatheca is a convoluted tube of relatively constant diameter with a terminal dictynoid pore and fertilization duct.

4. *Ethobuella tuonops* (Figs. 33-34). The atria in this species are paired and open at the anterolateral corners of a common, concave "scape." The copulatory ducts are extremely short, almost nonexistent. The spermathecae are somewhat complex, each having two anteriorly directed lobes with simple lumina and a larger posterior component with a compartmentalized lumen and a short, posterior fertilization duct. A single primary pore is on the anterior tip of the smaller of the two anterior lobes. The probable presence of a dictynoid pore is indicated by a nonconformity visible dorsally on the posterior component.
5. *Cryphoeca exlineae* (Fig. 35). The paired atria of this species are anteromedially located on the epigynum. They open into broad copulatory ducts which spiral anteriorly through more than 360°. The spermathecal head is a small anterolateral lobe bearing a single, posteriorly directed primary pore. At the anterior margin of the vulva the ducting (spermathecal stalk?) of each spermatheca turns posteriorly and passes through a very narrow bottleneck bearing an apparent dictynoid pore. This region is enveloped by the distal end of the copulatory duct making it difficult to verify the presence of the dictynoid pore. The remaining ducting (spermathecal base) is broad, slightly sinuous and bears a fertilization duct posteriorly.
6. *Neocryphoeca beattyi*, *N. gertschi* (holotype specimens in AMNH). New figures of the epigyna and vulvae of these species were not prepared for this study. The atrium in *N. gertschi* is transverse, posterior on the epigynum, and more or less single (being weakly continuous across the midline of the epigynum). The atria are similar in *N. beattyi* but are paired. Both species have sinuous, well sclerotized copulatory ducts proceeding anteriorly (Roth 1970, Figs. 2, 3). Close to the junction of each copulatory duct with a less well sclerotized spermatheca is a single anteriorly directed primary pore. These are visible ventrally and medially in the vulvae of *N. beattyi* and on the outer anterolateral vulval margins in *N. gertschi*. The spermathecae in the latter are large, relatively simple bulbs in which dictynoid pores have not been observed. The more complex and convoluted spermathecae of *N. beattyi* have a dictynoid pore hidden on the dorsal surface of an anteroventral blind lobe.

Taxa without dictynoid pores:

AGELENIDAE:

1. *Agelenopsis potteri* (Figs. 36-38). The vulvae of the species of *Agelenopsis* are complex. Their structure was described in detail by Gering (1953—various species) and Petrunkevitch (1925—*A. naevia*), but neither author noted the presence of primary pores distally on the "blind duct of the diverticle" (Figs. 37-38). Their "diverticle" is probably homologous to the spermathecal head. Both noted a primary pore bearing "blind tube" ventrally on the most heavily sclerotized component of the vulva. In *A. potteri* a similar "blind tube" is lacking but there are numerous primary pores ventrally on the heavily sclerotized component close to the exit of the fertilization duct (Fig. 36).

AMAUROBIIDAE:

1. "*Coelotes*" sp. (Fig. 41), in CNC; *Coras juvenilis* (Fig. 39); *Wadotes calcaratus* (Fig. 40). These three representatives of the coelotines all possess primary pores on more (Figs. 39-40)

or less (Fig. 41) well developed, lobe-like, spermathecal heads. The spermathecal ducting in *Wadotes* and especially in *Coras* becomes increasingly sclerotized and complex distally. The compact and very heavily sclerotized nature of the entire vulva in the "*Coelotes*" species examined precluded the complete determination of the complex duct trajectories.

2. *Callioplus macarius* (Fig. 44). In this species the vulva is very simple, compact, and heavily sclerotized. A small number of primary pores are located medially on the outer lateral margin of each spermatheca.

DICTYNIDAE:

1. *Dictyna coloradensis*. Unfortunately no good illustrations of the vulva of this species appear to exist and none was made during its examination for this study. Chamberlin and Gertsch (1958, pl. 26 Fig. 4) figured only the epigynum with its paired atria. Both they (Chamberlin and Gertsch 1958, various figs.) and Roberts (1985, Fig. 14) did publish figures of the vulvae of some other species of *Dictyna* but either the species figured lack or (more likely) these authors missed observing spermathecal heads as possessed by *D. coloradensis*. In this species primary pores are located distally on a relatively long, loosely coiled, membranous tube attached to each copulatory duct near the atria. This structure is easily overlooked and is presumed to exist in some form in other species of *Dictyna*.

LYCOSIDAE:

1. *Hogna helluo* (Figs. 42-43). In common with many other lycosines (see figures in Dondale and Redner 1990) this species has an anteriorly directed lobe distally on each spermatheca. In this species (and probably all the other lycosines with this feature) the lobe bears primary pores and is here considered to be the spermathecal head.

LIOCRANIDAE:

1. *Phrurotimpus borealis*, in CNC. This species is similar to *Agelenopsis potteri* in that it possesses two sets of primary pores. Here, however, they are located together on the most posterior and heavily sclerotized component (spermatheca?) of the vulva (see Dondale and Redner 1982, Fig. 246). The outer anterolateral margin of each spermatheca bears a single primary pore on the apex of a small nipple. The dorsal surface of each spermatheca is liberally scattered with other primary pores.

Discussion

This study provides further support for the hypothesis of primitive presence of primary pores in the vulva of all spiders. All spiders examined specifically for these structures have them. Dictynoid pores are present in all the dictynoid taxa examined so far except for *Neocryphoeca gertschi* and *Dictyna*. Some putative dictynoid groups such as the desids and anyphaenids have not been examined for this character.

Among spiders usually considered to be non-dictynoid, dictynoid pores have been found in *Tegenaria* (Agelenidae) (Figs. 25-30) and *Rubrius* (Amaurobiidae) (Fig. 21). Perhaps these two genera would be better placed in Dictynoidea. *Tegenaria* has traditionally been considered an agelenid because of its possession of plumose hairs, elongated posterior spinnerets, and a single row of tarsal trichobothria increasing in length distally. The first and third characters are plesiomorphic (see discussions in Bennett 1991:35-36 and especially Coddington 1990b:7; Fig. 3,

characters 8 and 9; and Table 1, character 49) and the second is too variable and poorly defined to be diagnostic. *Rubrius* was transferred from the Agelenidae (Cybaeinae) to the Amaurobiidae (Macrobuninae) by Lehtinen (1967) (i.e., from Dictynoidea to Amaurobioidea) apparently on the basis of overall similarity not apomorphy. However, at this point neither *Tegenaria* nor *Rubrius* can be placed in a specific dictynoid family (as opposed to Dictynoidea *incertae sedis*). Until other character systems such as trichobothria and spinneret spigots are analyzed for these taxa it is preferable to consider their possession of dictynoid pores as homoplasy and leave them in their current placements with the knowledge that their sister taxa may be dictynoid and not amaurobioid.

Coddington (1990a) postulated the following cladistic relationship: (Amaurobioidea (Dictynoidea, Orbiculariae)). No Orbiculariae were specifically examined for dictynoid pores but published SEM and compound microscope photographs of the vulvae of various orbicularian taxa (e.g. *Latrodectus*, Foelix 1982; Anapidae, Platnick and Forster 1989) show no indication of any structure comparable to a dictynoid pore. This, coupled with discussions with current students of orbicularian systematics, indicates that dictynoid pores do not exist in Orbiculariae.

Coddington (1989) proposed that possession of a highly branched tracheal system is an apomorphy of Dictynoidea *sensu* Forster (1970). I suggest that the dictynoid pore is a second apomorphy of Dictynoidea or at least those dictynoid families in which this pore has been observed.

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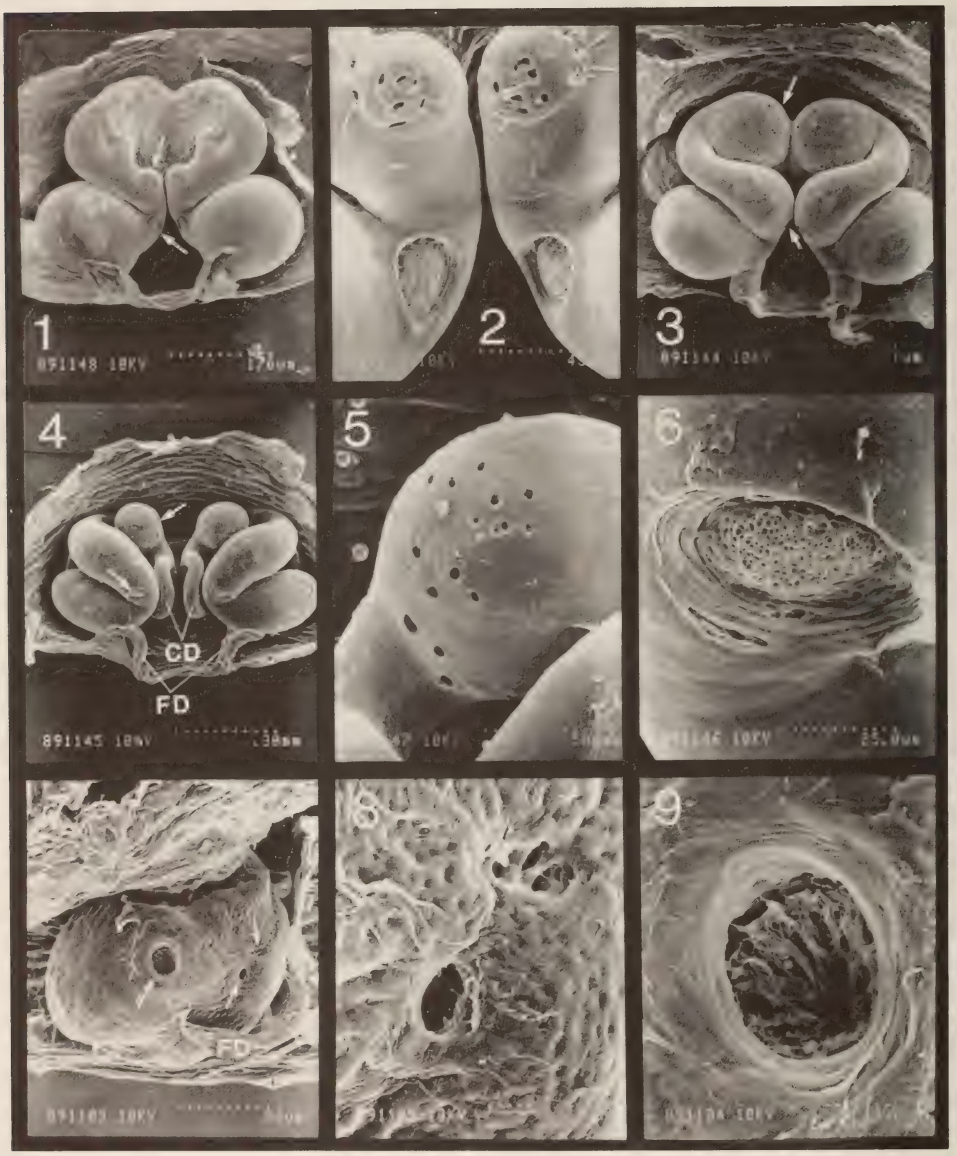
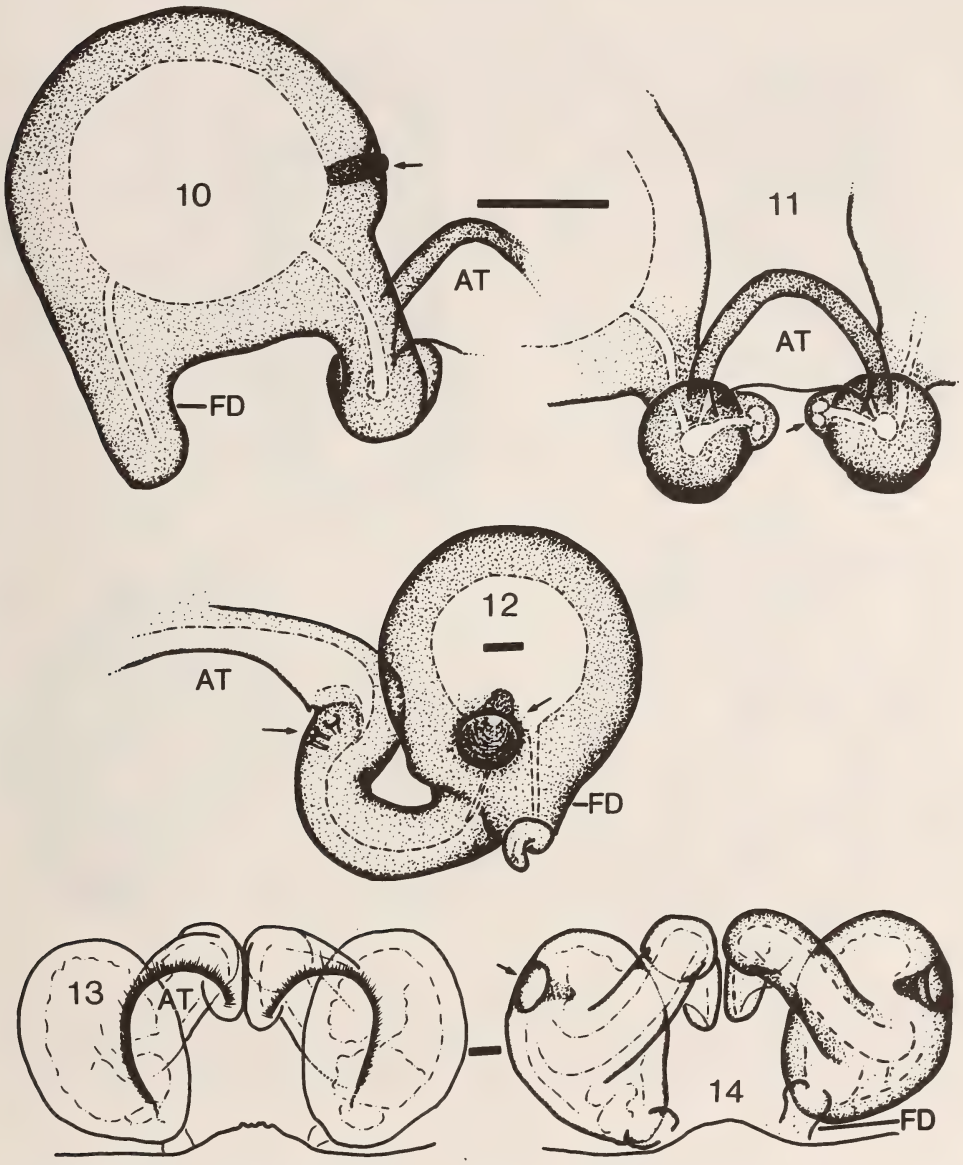
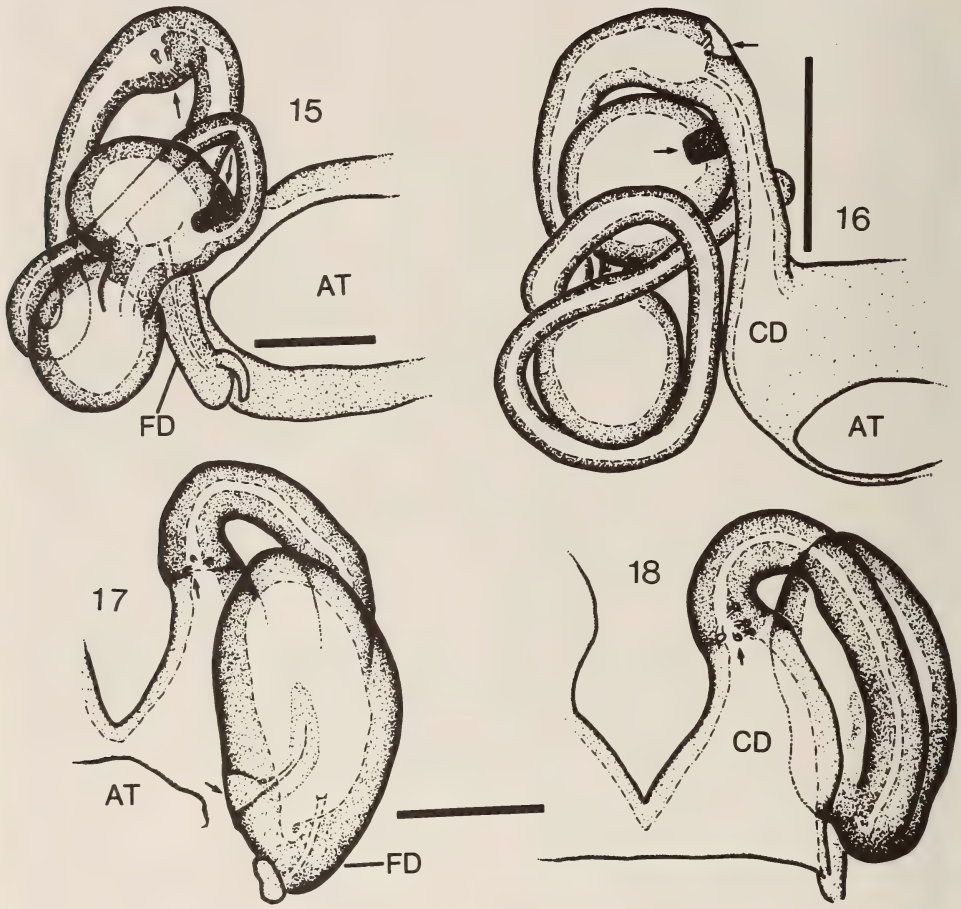


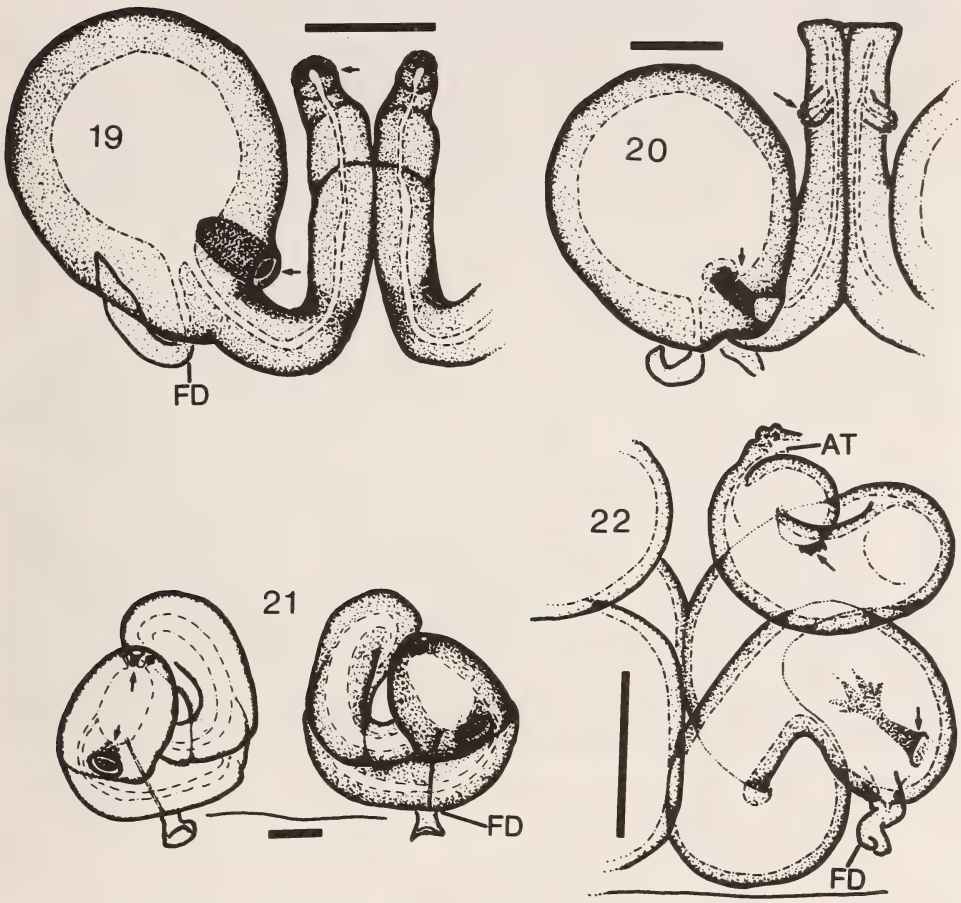
FIGURES 1-9. Vulvae and pores: 1, *Cybaeus grizzlyi*, dorsal; 2, detail of Fig. 1; 3, *Cs. morosus*, dorsal; 4, *Cs. signifer*, dorsal; 5, detail (primary pores) of Fig. 4; 6, detail (dictynoid pore) of Fig. 4; 7, *Argyroneta aquatica*, one-half of vulva, anterodorsal; 8, detail (primary pores) of Fig. 7; 9, detail (dictynoid pore) of Fig. 7. Arrows indicate pores. CD—copulatory ducts, FD—fertilization ducts.



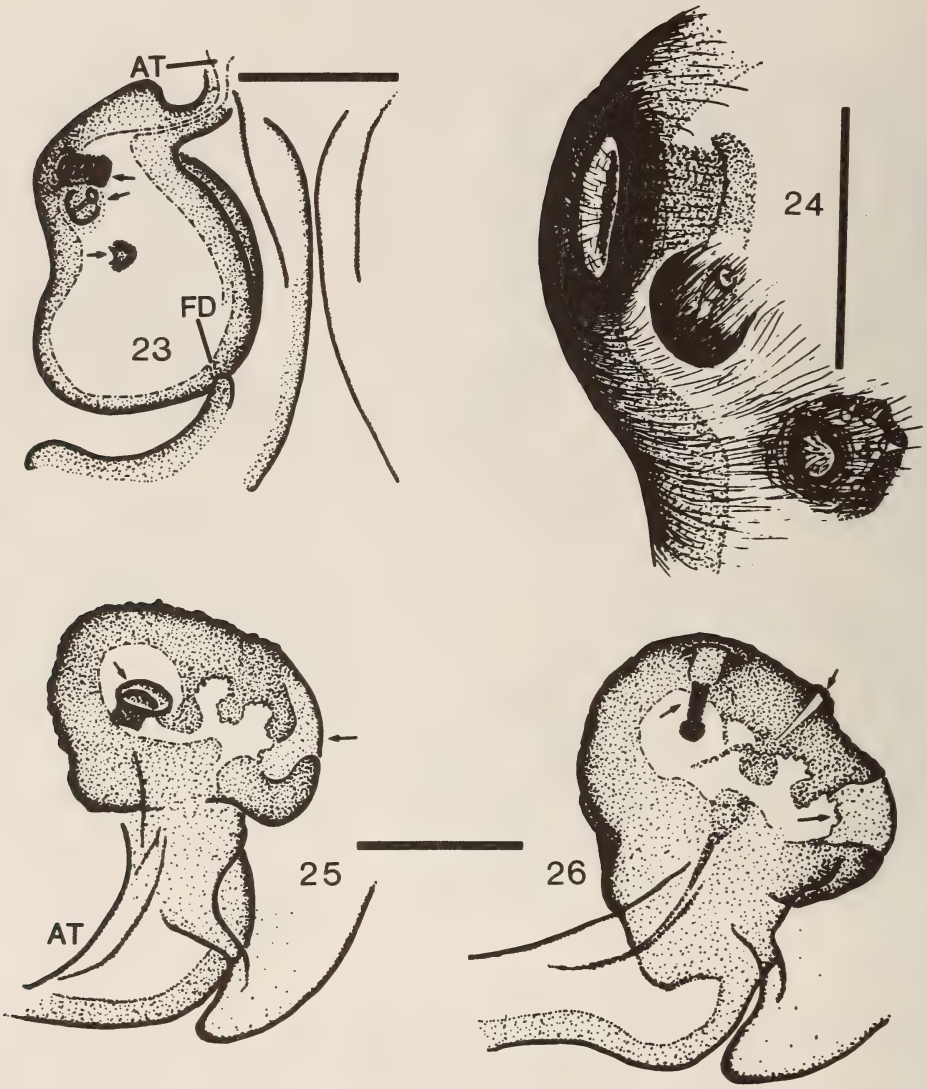
FIGURES 10-14. Vulvae and pores: 10, *Cybaeota shastae*, Victoria BC, dorsal; 11, same, ventral; 12, *Blabomma californica*, Victoria BC, dorsal; 13, *Yorima angelica*, Baja California, ventral; 14, same, dorsal. Arrows indicate primary and dictynoid pores. Scale bars = 0.025 mm. AT—atrium.



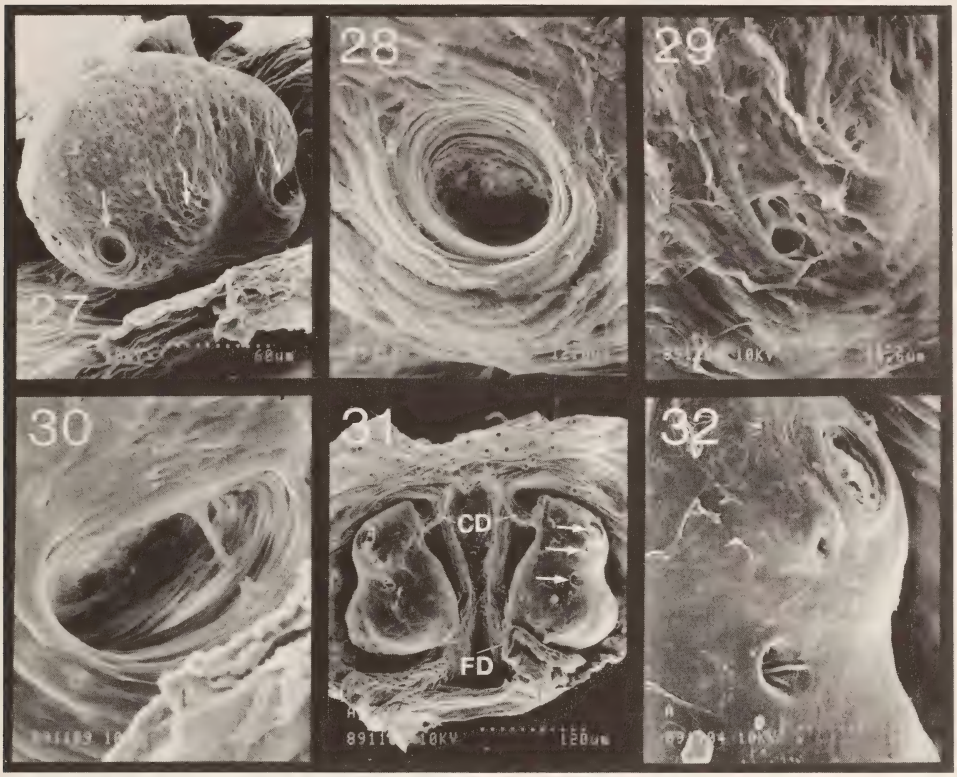
FIGURES 15-18. *Cicurina* spp., vulvae and pores: 15, *C. intermedia*, Wallowa Co. OR, dorsal; 16, *C.* nr. *cavealis*, St. Lawrence Is. Nat. Pk. ON, ventral; 17, *C. bryantae*, Graham Co. NC, dorsal; 18, same, ventral. Arrows indicate primary and dictynoid pores. Scale bars = 0.10 mm.



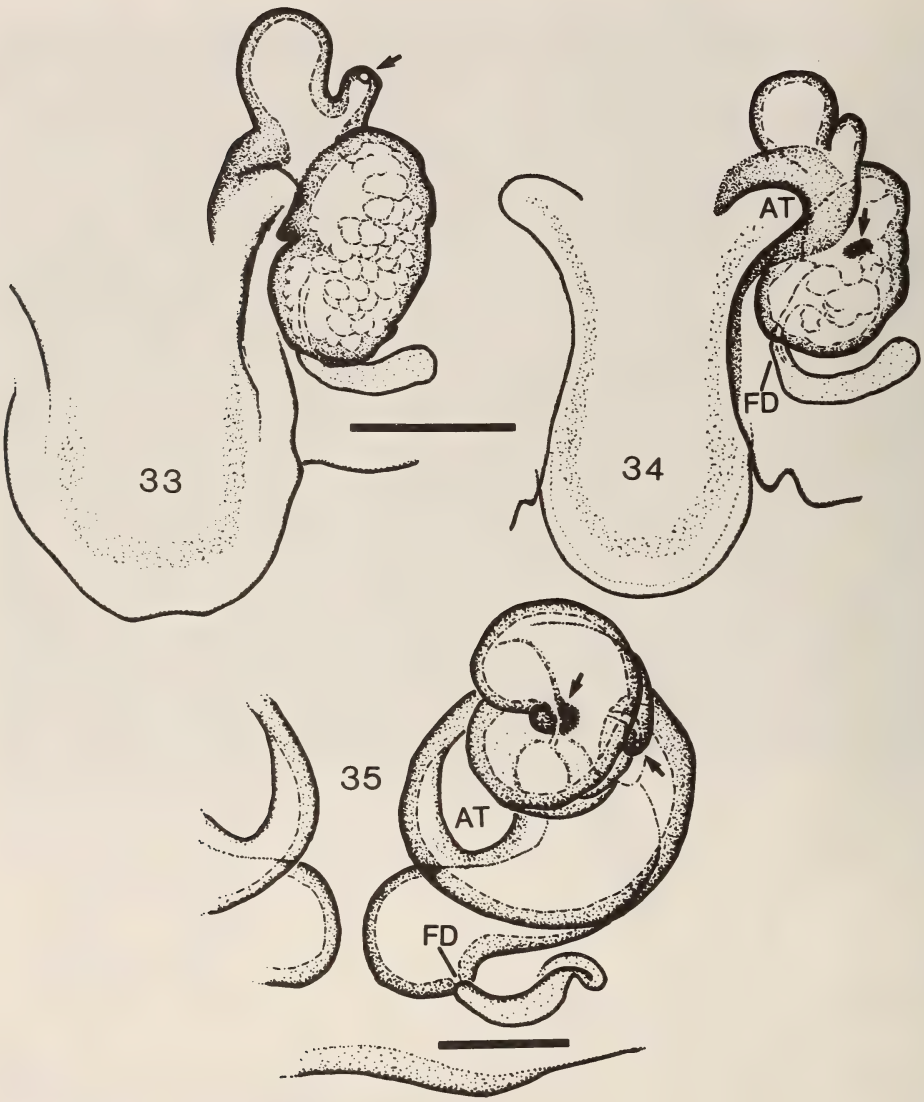
FIGURES 19-22. Vulvae and pores, dorsal: 19, *Calymmaria* sp., Skamania Co. WA; 20, *C. montavencis*, Great Smoky Mtn. Nat. Pk. NC; 21, *Rubrius antarcticus*, Isla Guarello, Magallanes, Chile; 22, *Neoantistea* sp., Great Smoky Mtn. Nat. Pk. NC. Arrows indicate primary and dictynoid pores. Scale bars = 0.10 mm.



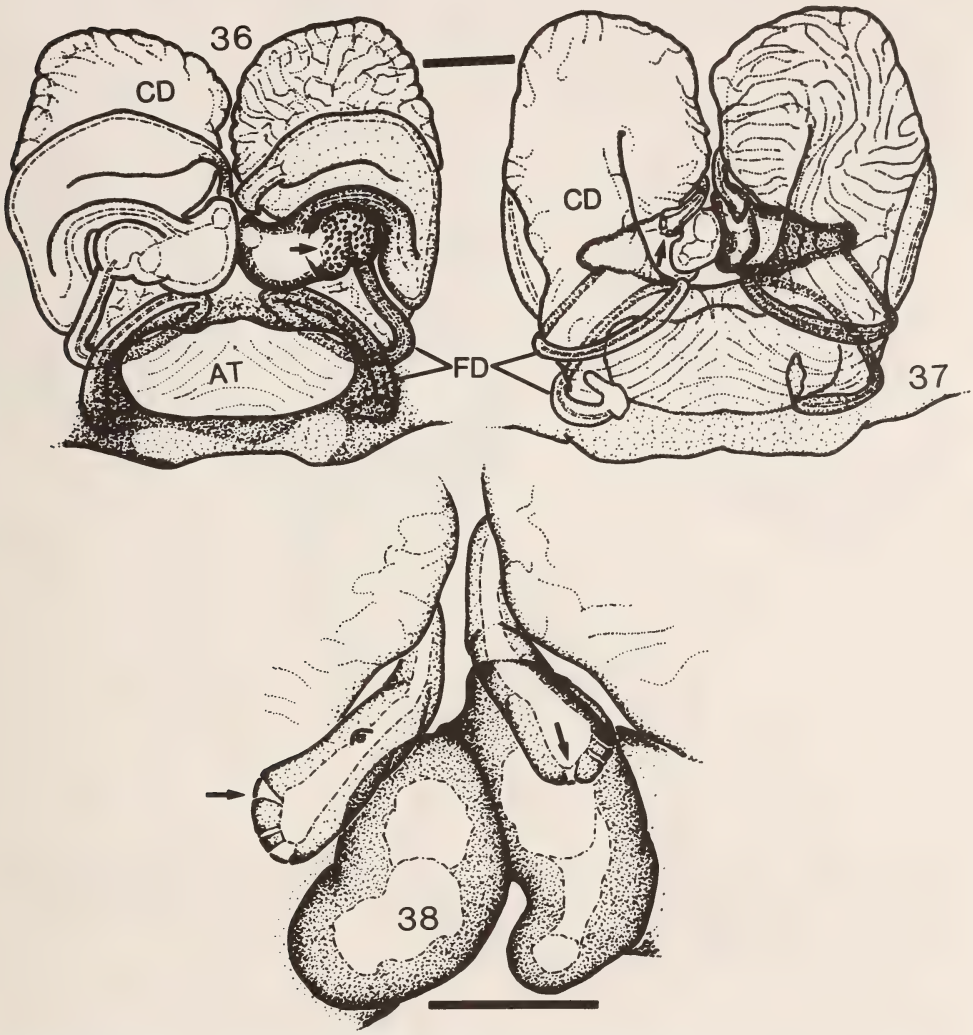
FIGURES 23-26. Vulvae and pores: 23, *Dirksia cinctipes*, North Vancouver BC, dorsal; 24, detail of Fig. 23; 25, *Tegenaria domestica*, Victoria BC, ventral; 26, same, Saanich BC, ventral. Arrows indicate primary and dictynoid pores. Scale bars = 0.05 mm.



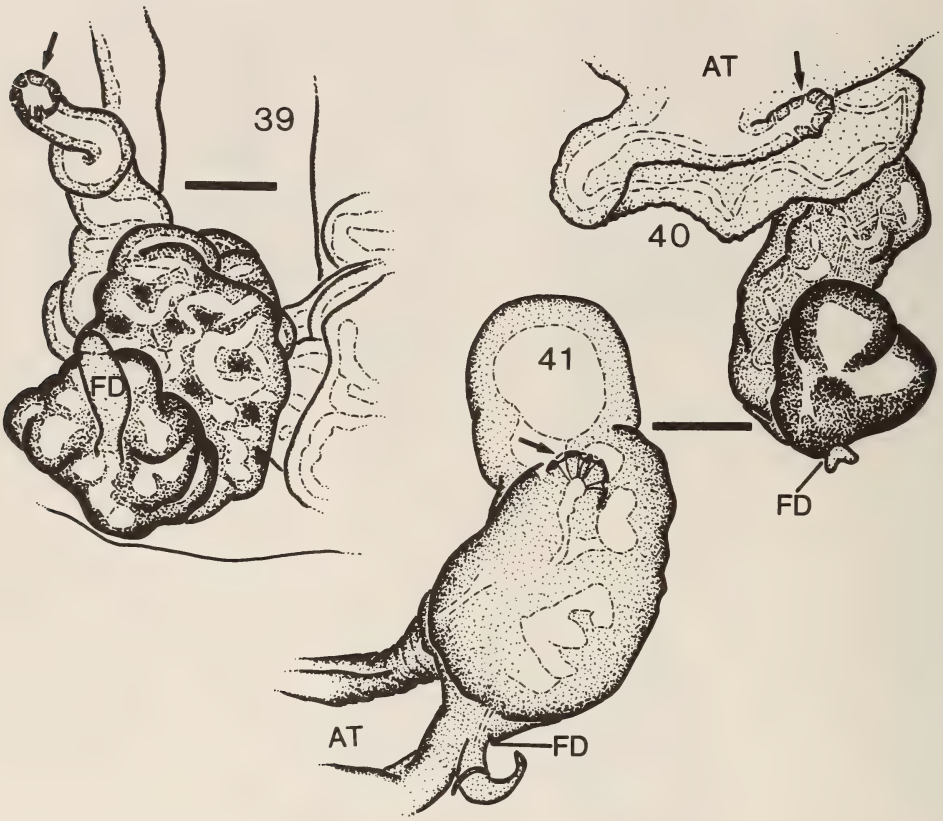
FIGURES 27-32. Vulvae and pores: 27, *Tegenaria domestica*, one-half of vulva, anterodorsal; 28-30, details of Fig. 27; 31, *Dirksia cinctipes*, dorsal; 32, detail of Fig. 31. Arrows indicate pores.



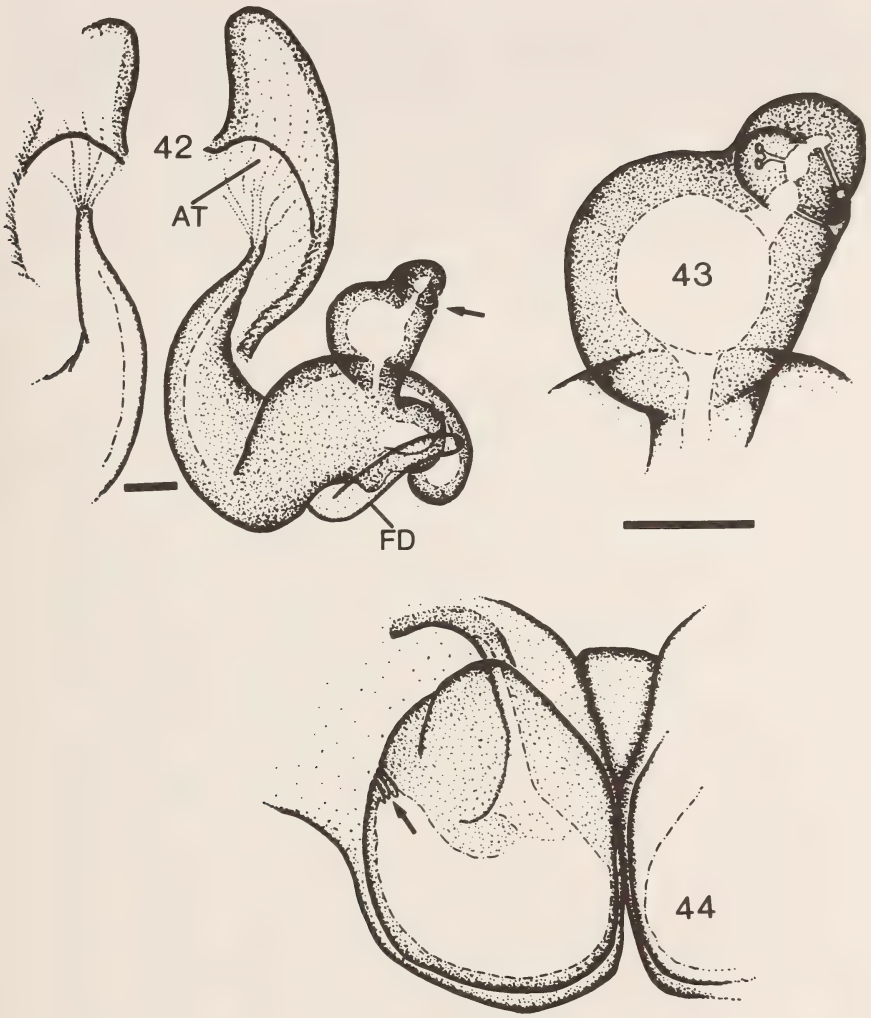
FIGURES 33-35. Vulvae and pores: 33, *Ethobuella tuonops*, Victoria BC, dorsal; 34, same, ventral; 35, *Cryphoeca exlineae*, Glacier Nat. Pk. BC, dorsal. Arrows indicate primary and dictynoid pores. Scale bars = 0.10 mm.



FIGURES 36-38. Vulva and pores, *Agelenopsis potteri*, Guelph ON: 36, ventral; 37, dorsal; 38, detail of Fig. 37. Arrows indicate pores. Scale bars = 0.10 mm.



FIGURES 39-41. Vulvae and pores, Coelotinae: 39, *Coras juvenilis*, Furnessville IN, dorsal; 40, *Wadotes calcaratus*, Halton Co. ON, anterodorsal; 41, "*Coelotes*" sp., near Ghopte Nepal, dorsal. Arrows indicate primary pores. Scale bars = 0.10 mm.



FIGURES 42-44. Vulvae and pores, dorsal: 42, *Hogna helluo*, Port Carling ON; 43, detail of Fig. 42; 44, *Callioplus macarius*, Lane Co. OR. Arrows indicate primary pores. Scale bars = 0.10 mm.

THE SUBGENERA, SPECIES GROUPS, AND SYNONYMS OF *ANAPHES* (HYMENOPTERA: MYMARIDAE) WITH A REVIEW OF THE DESCRIBED NEARCTIC SPECIES OF THE *FUSCIPENNIS* GROUP OF *ANAPHES S.S.* AND THE DESCRIBED SPECIES OF *ANAPHES* (*YUNGABURRA*)

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Abstract *Proc. ent. Soc. Ont.* 123:23-110

The genus *Anaphes* Haliday is redescribed and classified into two subgenera: *Anaphes s.s.* and *Anaphes* (*Yungaburra* Girault). Two species groups are recognized in *Anaphes s.s.* - the *fuscipennis* group (previously *Anaphes s.s.*) and the *crassicornis* group (previously *Patasson* Walker). Three species groups are recognized in *A.* (*Yungaburra*) - the *amplipennis* group [previously *A.* (*Austranaphes* Ogloblin)], the *nitens* group (previously *Yungaburra s.s.*), and an unnamed group based on undescribed species principally from New Zealand. A phylogeny is proposed in which the subgenus *Yungaburra*, with an austral disjunct distribution, is hypothesized to be the primitive sister group and the more derived subgenus *Anaphes* occurs principally in the Northern Hemisphere.

Descriptive notes are provided for the type species of 9 of the 14 synonyms of *Anaphes*, based on study of their primary type specimens. Lectotypes are designated for *Anaphes pratensis* Förster and *Hofenederia* ***pectoralis*** Soyka. The following new synonymies are proposed: *A. ranalteri* (Soyka) and *A. lacensis* (Soyka) under *A. medius* Soyka; *A. pinguicornis* (Soyka) under *A. pectoralis* (Soyka); *A. capitulata* (Soyka), *A. filicornis* (Soyka), *A. maculata* (Soyka), *A. neopratensis* (Soyka), and *A. stammeri* (Soyka) under *A. fuscipennis* Haliday; *A. lemae* Bakkendorf under *A. flavipes* Förster; and *A. neuquenensis* Ogloblin under *A. pucarobius* Ogloblin. Keys are given to the subgenera and species groups of *Anaphes*. The 9 described Nearctic species of the *fuscipennis* group are reviewed and keyed. The 6 descibed species of *A.* (*Yungaburra*) are keyed. One new species, *A.* (*Anaphes*) *byrrhidiphagus*, is described. A checklist of 250 nominal species of *Anaphes* is given, 16 of which were previously assigned to other genera. Two species are removed here from *Anaphes* to *Erythmelus* Enock, as new combinations: *Erythmelus harveyi* (Girault) and *E. tingitiphagus* (Soares). *Anaphes foersteri* Ratzeburg is provisionally assigned to *Anagrus* but its true placement may never be determined because its type specimen(s) were destroyed.

Résumé *Proc. ent. Soc. Ont.* 123:23-110

Le genre *Anaphes* est redécrit et classifié en deux sous genres: *Anaphes s.s.* et *A.* (*Yungaburra*). Deux groupes d'espèces sont reconnus a l'intérieur d'*Anaphes s.s*, le groupe *fuscipennis* (préalablement *Anaphes*) et le *groupe crassicornis* (préalablement *Patasson*). Trois groupes d'espèces sont reconnus a l'intérieur d'*A.* (*Yungaburra*) - le groupe *amplipennis* (préalablement *Austranaphe*), le groupe *nitens* (préalablement *Yungaburra s.s.*), et un groupe sans nom basé sur des espèces non décrites principalment de la Nouvelle Zélande. Les groupes d'espèces à l'intérieur de chaque sous genre sont séparable dans les femelles seulement, selon le nombre d'articles de la massue. Une phylogénie est proposée dans laquelle *Yungaburra*, avec une distribution disjoncte Australe, est considerée comme le sous genre ancestral et le sous genre *Anaphes* plus dérivé se trouvent principalment dans l'hémisphère nord.

Des notes descriptives sont données pour les espèces types de 9 des 14 symonymes d'*Anaphes* basées sur l'étude de leurs types primaires. Des lectotypes ont été désignés pour *Anaphes pratensis* Förster et *Hofenederia* ***pectoralis*** Soyka. Les synonymes nouveaux suivants sont proposés: *A. ranalteri* (Soyka) et *A. lacensis* (Soyka) sous *A. medius* Soyka; *A. pinguicornis* (Soyka) sous *A. pectoralis* (Soyka); *A. capitulata* (Soyka), *A. filicornis* (Soyka), *A. maculata* (Soyka), *A. neopratensis* (Soyka,) et *A. stammeri* (Soyka) sous *A. fuscipennis* Haliday; *A. lemae* Bakkendorf sous *A. flavipes* Förster; et *A. neuquenensis* Ogloblin sous *A. pucarobius* Ogloblin. Nous présentons des clés aux sous genres et groupes d'espèces d'*Anaphes*. Les 9 espèces Néarctiques décrites du group *fuscipennis* sont revues et une clé est présentée. Une clé est presentée pour distinguer les 6 espèces décrites d'*A.* (*Yungaburra*). Une nouvelle espèce, *A. byrrhidiphagus*, est décrite. Une liste de 250 espèces nominales d'*Anaphes* est donnée, 16 desquelles ont été placé dans d'autres genres. Deux espèces sont enlevées d'*Anaphes* et placées dans des combinaisons nouvelles: *Erythmelus harveyi* (Girault) et *E. tingitiphagus* (Soares). *Anaphes foersteri* Ratzeburg est provisoirement placé dans *Anagrus* mais son emplacement réel probablement ne sera jamais déterminé parce que les spécimens types ont été détruit.

Introduction

The genus *Anaphes* is one of the more speciose genera of Mymaridae, containing 231 nominal species (checklist p. 72). Members of the genus are egg parasites mainly of Curculionidae and Chrysomelidae, but there are literature reports, some of doubtful accuracy, of *Anaphes* species parasitizing members of 17 additional families of insects (Huber 1986). Four species of *Anaphes* have been used, sometimes successfully, for the biological control of important agricultural and forestry pests in several countries (Clausen 1978; Huber 1986) and there is continued interest in using other members of this genus in more biological control programs (Boivin 1986; Collins and Grafius 1986; Aeschlimann 1986; Jackson 1986; Aeschlimann *et al.* 1989; Dysart 1990). The result has been a relatively large volume of applied literature on at least seven species of the genus.

Unfortunately, for reasons discussed below, specific names used in the biological literature are sometimes incorrectly applied to the species studied.

Despite their proven importance in biological control, the taxonomy of *Anaphes* is in a very poor state. Most species are unrecognizable from the descriptions alone, there are no recent revisions of the genus, and species identification is difficult so that relatively few species are correctly identifiable using existing keys. In addition, one species, *A. iole* Girault, has been reared from two different hosts and significant host-induced morphological variation was obtained (Huber and Rajakulendran 1988), thus adding another complication to species recognition and definition. In contrast, many species appear to be so similar that they cannot be distinguished reliably using morphological characters alone. A thorough re-evaluation of previously described species is therefore needed.

The purpose of this paper is to review the infrageneric groups of *Anaphes* worldwide, to redescribe, illustrate, and key the previously described North American species of the *fuscipennis* group so as to make them identifiable, and to review the described species of *A.* (*Yungaburra*). Although there are clearly many undescribed species of *Anaphes* it seems pointless at this stage in our knowledge of the taxonomy of the genus to describe them unless accurate host records are available and/or there is a real need to publish a new scientific name. In the single instance where I describe a new species it is because specimens were reared from known hosts, a good series of specimens was available for study, and the species was morphologically quite distinct from any previously described species.

Methods

Approximately 3000 pinned or slide mounted specimens were examined during this study. The types of each species discussed were examined unless otherwise indicated. The method of preparing specimens, discussion of terms used and measurements made follow Huber (1987, 1988). Terms which were not discussed previously are the marginal and medial spaces ("Marginalraum" and "Medialraum" of Soyka, 1949), defined here as the two, usually distinct, hairless areas of the fore-wing blade in front of the cubital row of microtrichia (Figs. 6, 7, 20-36). Measurements are given in micrometers (µm), with the mean followed, in parentheses, by the range and number of specimens measured. Measurements of primary types are given in Appendices I and II. Abbreviations used in the descriptions are: F = funicular article; T = abdominal tergite; FWL, FWW, HWL, HWW, LMC = fore wing length and width, hind wing length and width, and longest marginal cilia, respectively. Many of the specimens studied were preserved for varying periods of time in alcohol before being point- or slide-mounted and consequently are often somewhat faded. Therefore, the colour given in the descriptions is often not quite accurate. In life the specimens may be darker in colour than described.

This study is based on specimens loaned from the following institutions:

BMNH - The Natural History Museum, London. J.S. Noyes.
CISC - University of California, Berkeley. L.E. Caltagirone.
CNCI - Canadian National Collection of Insects, Ottawa. J. Huber.
CUIC - Cornell University, Ithaca. J.K. Liebherr.
DEBU - University of Guelph, Guelph. S. Marshall.
EMUS - Entomological Museum, Utah State University, Logan. G.E. Bohart.
INHS - Illinois Natural History Survey, Urbana. K.C. McGiffin.

LACM -	Los Angeles County Museum of Natural History, Los Angeles. R.R. Snelling.
MLPA -	Museo de la Plata, La Plata. R.A. Ronderos.
MHNG -	Muséum d'Histoire Naturelle de Genève, Geneva. C. Besuchet.
MZUF -	Museo Zoologico de "La Specola", Florence. S. Mascherini.
NHMW -	Naturhistorisches Museum Wien, Vienna. M. Fischer.
NMID -	National Museum of Ireland, Dublin. J.P. O'Connor.
OSUO -	Oregon State University, Corvallis. P. Hanson
PMAE -	Provincial Museum of Alberta, Edmonton. A.T. Finnamore.
ROME -	Royal Ontario Museum, Toronto. C. Darling.
UCRC -	University of California, Riverside. J. Hall.
UICM -	University of Idaho, Moscow. F.W. Merickel.
USNM -	United States National Museum, Washington. M.E. Schauff.
ZMUC -	University of Copenhagen, Copenhagen. B. Petersen.

Historical Review

The nomenclatural history of *Anaphes* is well discussed and summarized by Debauche (1948), Annecke and Doutt (1961), Graham (1982), and Schauff (1984a), so is not repeated here. Not all problems have yet been resolved, however. As pointed out by Graham (1982: 204), *Ichneumon punctum* Shaw, established as type species of the genus *Anaphes* in ICZN Opinion 729 (China 1965), cannot be identified. *A. fuscipennis* Haliday was treated as the type-species of *Anaphes* by some earlier workers, e.g., Ashmead (1904), Debauche (1948, 1949), and Hellén (1974). It would be useful if the previous designation of *I. punctum* as type-species were set aside by the International Commission on Zoological Nomenclature and *A. fuscipennis* were to be adopted as the type-species of the genus, as recommended by Graham (1982).

Anaphes is a very homogeneous genus although past workers attempted to classify the species into numerous genera or subgenera. Most workers currently recognize only one genus with at most two subgenera.

Of the 231 nominal species included here in *Anaphes* about 66% (153) were described from Europe by Soyka (1946a, 1946b, 1949, 1950, 1953a, 1953b, 1954, 1955). Soyka divided the species among nine genera which were explicitly or implicity synonymized under *Anaphes s.l.* by later workers. Debauche (1948) and Soyka (1949, 1953b) keyed Belgian species and most of the European species, respectively. Hellén (1974) keyed the species of Finland. Tryapitzin (1978) provided a Russian translation of Debauche's keys which was subsequently translated into English (Tryapitzin 1987). Species described from regions other than Europe include 18 from North America, five from South America (four keyed in Ogloblin 1962), eight from Australia, three from Africa, and one from Japan.

The North American species of *Anaphes* were catalogued as two genera, *Anaphes* and *Patasson*, by Burks (1979). Ten of the species considered native to the continent were described by Girault (1905, 1909, 1910, 1911e, 1916, 1929). Three Palaearctic species were accidently (*A. fuscipennis*) or intentionally (*A. luna*, *A. flavipes*) introduced from Europe into North America for biological control of agricultural pests (Clausen 1978; Huber 1986). Attempts have been made to establish a fourth species, *Anaphes diana* Girault, from Europe (Yeargan and Shuck 1981). Girault (1910, 1911e, 1929) provided keys to the North American species but they are incomplete and difficult to use. Doutt (1949) provided a key to the species of *A.* (*Patasson*) (as *Anaphoidea*).

Problems in Species Recognition

I cannot place confidently under existing species names several hundred point- or slide-mounted specimens of the total number that I examined. Many of these may represent undescribed species but I do not describe them here for two reasons.

First, intraspecific variation occurs which cannot easily be distinguished from interspecific differences. Some species of *Anaphes* are known to produce more than one parasite from a single host egg (multiparasitism). The size of these parasites can vary considerably depending on how many develop per egg. Very small specimens may not be identifiable, unless associated by rearing with larger individuals from the same egg. Also, as mentioned above, host induced structural variation occurs in *Anaphes iole* Girault (Huber and Rajakulendran 1988). Because discontinuous variation is possible in at least one *Anaphes* species, and may occur in other species of *Anaphes* for which hosts are still unrecorded, great care must be taken in describing new taxa. Cross-breeding experiments in which *Anaphes* reared from one host are transferred to others and the morphology of the specimens reared from the different hosts is compared would be very useful in helping to elucidate species limits and amount of intraspecific variation possible. Attributes that appear to separate the described species often are very minor and difficult to describe adequately. These differences may only represent infraspecific variation but because of lack of biological information and sufficiently long series for study it is often not possible to distinguish interspecific from intraspecific variation.

Second, numerous species, most of which are not identifiable with any confidence using the existing literature, have been described from Europe. Quite probably, many of these names will be synonymized under one another. It is necessary that the nominal taxa be adequately studied, using large amounts of fresh, well prepared material for comparison with the types, and infraspecific variation be taken into account, before any species are described from North America. Otherwise, it is likely that at least some of the species described from North America will be the same and will eventually have to be synonymized.

In consequence, I see little point in describing new species of *Anaphes* unless required to provide a name for an economically important species because so many of the previously described species remain unidentifiable.

Distribution

The genus *Anaphes* is worldwide but species and numbers of individuals appear to be much more numerous in temperate and cold areas (i.e. higher latitudes) compared with the tropics. The genus appears to be poorly represented in the Afrotropical region. The greatest structural diversity occurs in the Australian region.

Maximum northern and southern collection records are, respectively: an undetermined specimen of *Anaphes* in the *crassicornis* group from Canada, NWT, Hazen Camp, 81º49'N, 70º18'W, 7.VII.1963, R.E. Leech (1♀, CNC); and *Anaphes nunezi* Ogloblin from Argentina, Tierra del Fuego, Bahía Aguirre, 54º57'S, 65º50'W, 14.II.1949, J. Núñez (1♀ and 1♂, LaPlata) (Ogloblin 1962). These two records also represent the furthermost northern and southern distribution records for the family Mymaridae. In high latitudes (beyond the tree line) the only mymarids present are species of *Anaphes* (e.g. Danks 1983) with one exception (*Notomymar*) in the southern hemisphere (Block 1992).

Biology and Economic Importance

In the family Mymaridae, several species of *Anaphes* are among the better studied biologically, mainly because of their actual or potential use in biological control of important pests. Much of the non-taxonomic literature on the genus is on relatively few species such as *A. conotracheli*, *A. diana*, *A. flavipes*, *A. fuscipennis*, *A. iole*, *A. luna*, *A. nitens* and *A. sordidatus* which have proved to be important in natural or biological control.

Anaphes species are mostly parasites of Curculionidae and Chrysomelidae, but there are a few records from other families of insects. A list of hosts, a summary of the use of several species in biological control projects of varying success, and a brief review of important papers on the biology of some of the species was given by Huber (1986). Hopkins (1978) reviewed the literature on some important species. Because Coleoptera are relatively uncommon at high latitudes where species of *Anaphes* are often common it is possible that Diptera are the main hosts there, but this is yet to be determined for certain.

Except for a few species that parasitize host eggs laid in vegetation such as plant stems, specimens of *Anaphes* are most frequently caught in pan traps. This is probably because many *Anaphes* parasitize eggs that are laid in or close to the soil. Other trapping methods are generally much less efficient in catching members of the genus.

Hurd (1954) implicated *Anaphes* sp. (as *Mymar*), among other insects, in a unique case of medical interest in which the author became ill as a result of aspirating several arthropods which infected his sinuses.

Relationships

Kryger (1934) and Debauche (1948) made the first critical analyses of *Anaphes* species and concluded that the attributes used to divide the genus were inadequate. Yet Kryger (1950) and Annecke and Doutt (1961) continued to treat *Anaphes* and *Patasson* as separate genera. Debauche (1948, 1949), Graham (1982), and Schauff (1984a) treated *Patasson* as a subgenus of *Anaphes*. All, however, agreed that the attributes used to separate *Patasson* from *Anaphes*, regardless of their hierarchical level, were not very good. Annecke and Doutt (1961) and Graham (1982) suggested that a division of *Anaphes* into subgenera was unsatisfactory because only one not-completely-reliable character was used and it applied to one sex only. Instead, they proposed that species groups would be more appropriate than subgenera for subdividing the relatively numerous species of *Anaphes*. In contrast, Soyka (1946b, 1949, 1950) subdivided *Anaphes* into several genera.

The genus is indeed very homogeneous, at least in the Holarctic region. The only way one can group the species in an almost non-arbitrary manner is by the number of flagellomeres, as was done by previous workers. Even using this character, some species may have to be arbitrarily assigned to one or other species group. Nevertheless, subgenera can still be usefully employed in *Anaphes*, though the division proposed below (Table I, Fig. 1) does not follow that used by earlier workers.

Subgenera, like genera, should reflect the evolutionary history of a group, irrespective of whether this history is expressed as morphological modifications in males or females, or both. Therefore, eliminating subgenera in *Anaphes* because the attributes used to subdivide the genus are based only on the female sex is not valid. For the most part, mymarid taxonomy, including that

TABLE I. Character matrix for species groups of *Anaphes*.

Present subgenus	Species group	Old subgenus	Female - # of club articles (# of sensory ridges on club)*	Male - sensory ridges on F1 (apparent # of flagellomeres)*
Yungaburra	unnamed	-	3 (8)	present (11)
Yungaburra	*nitens*	*Yungaburra*	2 (8) (some 6)	present (11 or 10)
Yungaburra	*amplipennis*	*Austranaphes*	1 (8)	present (11)
Anaphes	*crassicornis*	*Patasson*	2 (6)	absent (10)
Anaphes	*fuscipennis*	*Anaphes s. s.*	1 (6)	absent (10)

* The smaller number is considered to be the apomorphic state.

of *Anaphes*, is based on the female sex only. Males are generally ignored because few specific attributes occur in this sex to separate the species reliably. Nevertheless, the primary division of *Anaphes* into what are probably the two most well defined and natural groups, is based on a male character.

The evolutionary scenario proposed here to substantiate the subgenera and species groups is based on two assumptions: first, that reduction and (apparent) loss of flagellomeres represents a derived condition; second, before flagellomeres are reduced their complement of sensory ridges and setae is gradually lost. All flagellomeres in male antennae have at least one sensory ridge, unlike female antennae where sensory ridges are often reduced in number or absent from one or more flagellomeres.

I consider the primary division separating groups within *Anaphes* to be the apparent reduction from 11 to 10 flagellomeres in males. This apparent reduction in number has occurred by a gradual shortening of F1 with loss of sensory ridges and setae until F1 is, effectively, gone (Figs. 14, 16-18, 59, 60). In fact, there are 11 flagellomeres in all *Anaphes* species but reduction of F1 makes it appear that many species have only 10 flagellomeres. The important distinction is whether 11 or 10 flagellomeres in males have sensory ridges, i.e., whether F1 has one or more sensory ridges, or none. There is good evidence for this proposed transformation series. In many, mostly undescribed, species e.g., of the *amplipennis* and *nitens* group of species, F1 has the normal complement of sensory ridges and is almost as long as other flagellomeres (Figs. 15, 19). Thus, males clearly have 11 flagellomeres. Males of *A. nitens* (Girault), *A. inexpectatus* Huber and Prinsloo and *A. tasmaniae* Huber and Prinsloo have F1 very short (slightly wider that long), much shorter than any of the remaining flagellomeres, with one seta and one transverse sensory ridge (Figs. 18, 59). In other species, all belonging to *Anaphes s.s.*, there is a remnant of F1 which has one or two setae but no sensory ridge. This anelliform remnant is perhaps most noticeable in, e.g., *A. acutiventris* (Soyka) and *A. fuscipennis* (Figs. 16, 17) where the flagellomere is only slightly shorter than wide. In other species of *Anaphes s.s.* it is even shorter but a seta always seems to be present. These species therefore appear to have only 10 flagellomeres. Debauche (1948: 154) enumerated such anelliform flagellomeres in males and I agree with this practice. Therefore, as

mentioned above, all male *Anaphes* have 11 flagellomeres even though superficial examination of a male antenna of all species of *Anaphes s.s.* would suggest that only 10 flagellomeres are present.

In females there are always six funicular articles, and a club of one to three articles. Species with a club of three articles only occur in the Australian region. The club bears either 8 or 6 sensory ridges. F1 is always the shortest and never (? or rarely) bears sensory ridges. In the *amplipennis* and un-named groups of species F1 is longer than usual, more approximating the length of the remaining funicular articles (Figs. 11, 13).

If one accepts the primary division of *Anaphes* into subgenera based on presence or absence of at least 1 sensory ridge on F1 (11 or apparently 10 flagellomeres) in males, then any other character one examines will be found to be convergent in some species. For example, Debauche (1948) gave some attributes other than the divided versus entire club in females to separate *Anaphes s.s.* from *A.* (*Patasson*). These are (translated from French): *Anaphes s.s.* "includes generally larger species, with wider wings, tarsus with longer, often unequal, articles and, in females, the basal forward-produced ovipositor sac usually poorly developed; males generally have longer, more slender antennal articles". All these differences are relative and intergrade continuously among members of the two subgenera. The only attribute that I found as a useful complement to the antennal characters is the relatively longer basal anterior prolongation of the ovipositor (Fig. 69) in the *crassicornis* group which can help decide species group placement when the female club appears to be only partly divided or is not clearly visible.

The two subgenera treated here are further subdivided into five species groups. A classification of five subgenera would also be a possibility, but would connote undue structural diversity within the genus relative to other genera of Mymaridae. Although species groups are proposed here, four of the five groups have previously been proposed as genera or subgenera. Because tradition dies hard, biologists may prefer to continue using well known generic names such as *Patasson* for some of these groups, but a predictive, formal classification should have only a single set of names or else confusion and lack of nomenclatural stability result. Therefore, I would discourage use of such names.

The two fossil species of *Anaphes*, *A. splendens* Meunier and *A. schellwieniens* Meunier, described from oligocene amber (Meunier 1901) may not belong to this genus. The illustration of the fore wing of *A. splendens*, at least, certainly does not resemble the wing of any extant *Anaphes* species. I have not seen the type specimens and do not know where these two species would best be classified.

Four autapomorphies can be used to define *Anaphes*, three of the fore wing and one of the male genitalia. They are: the presence of a single dorsal seta on the fore wing blade just apical to the frenum (Fig. 6); the presence of marginal and medial spaces on the fore wing (Figs. 6, 7, 20-36); the asymmetrical lozenge-shaped margin of the apex of the fore wing (Figs. 20-36); and the male genitalia which are exposed ventrally, situated in a groove between the apical sternites which surround it laterally and dorsally (Figs. 5, 73-76). The wing apex asymmetry is not well defined in many members of *A.* (*Yungaburra*) (Fig. 8) and some species of *A.* (*Yungaburra*) appear to lack marginal and medial spaces, or have very small ones (Fig. 8). A cladogram of proposed relationships is given in Fig. 1. The number of club articles and the number of sensory ridges on the club of females is homoplasious. In the *nitens* group the three species with a very short F1 bearing only 1 sensory ridge also have only 6 sensory ridges on the club whereas the species of the *amplipennis* and unnamed groups have a longer F1 with several sensory ridges and 8 sensory ridges on the club. This would suggest that the *nitens* group is perhaps the most advanced within *A.* (*Yungaburra*), except that it has two instead on one club articles.

Although *Anaphes* is certainly monophyletic its relationship to other genera is not yet clearly determined. Schauff (1984a) placed *Anaphes* close to *Erythmelus* on the basis of a particular kind of metasomal attachment to the mesosoma. Viggiani (1988) placed *Anaphes* close to *Richteria* Girault on the basis of similar male genitalia. Noyes and Valentine (1989) proposed that *Anaphes* is most closely related to an undescribed genus (genus B) from New Zealand. I believe that the sister genus to *Anaphes* will certainly be found in the Australian region and probably in New Zealand as Noyes and Valentine (1989) suggested but I have no further information to add since their publication. Further study of the group of genera included by Noyes and Valentine (1989) in subgroup "d" of their *Anaphes* group is needed to resolve the relationships of *Anaphes*.

Taxonomy

Anaphes Haliday

Anaphes Haliday 1833: 346; Walker 1846: 50; Schmiedeknecht 1909: 499; Girault 1911e: 287; Gahan and Fagan 1923: 12; Hincks 1944: 38; Soyka 1946b: 180; Debauche 1948: 154; Gahan 1949: 204; Kryger 1950: 39; Debauche 1949: 63; Soyka 1955: 460; Annecke and Doutt 1961: 26; China 1965: 82; Viggiani 1973: 273; Hellén 1974: 23; Graham 1982: 202; Schauff 1984a: 46; ICZN 1987: 45; Noyes and Valentine 1989: 26; Yoshimoto 1990: 50.

Type-species: *Ichneumon punctum* Shaw 1798: 189, by subsequent designation (Westwood 1839: 78). Fixed by ICZN, Opinion 729 (China 1965). Type specimen(s): lost, and unrecognizable from original description. (See discussion above regarding formal designation of a new type species).

Panthus Walker 1846; 50; Gahan and Fagan 1923: 103; Kryger 1950: 81; Soyka 1955: 460 (as *Pantjus*, misspelling); Graham 1982: 202.

Type-species: *Panthus crassicornis* Walker 1846: 52, by subsequent designation (Gahan and Fagan 1923: 103). Type specimen: lectotype ♀ (NMDI) designated by Graham (1982) [not examined]. Synonymized formally by Graham (1982) (already treated as synonym, in part, of *Anaphes* by Debauche (1948: 154, 1949: 63). Member of *crassicornis* group.

Patasson Walker 1846: viii; Girault 1910: 246; Kryger 1934: 507; Ogloblin 1939: 144; Debauche 1948: 156; Debauche 1949: 64; Kryger 1950: 84; Hincks 1960: 213; Annecke and Doutt 1961: 21; Viggiani 1973: 273; Graham 1982: 210; Schauff 1984a: 48.

Type-species: *Panthus crassicornis* Walker 1846: 52, by monotypy. Type specimen: lectotype ♀ (NMID) designated by Graham (1982) [not examined]. Synonymized under *Anaphes* by Debauche (1948: 154). Member of *crassicornis* group.

Flabrinus Rondani 1877: 180; Gahan and Fagan, 1923: 65; Hincks 1944: 38; Debauche 1948: 233; Gahan 1949: 205; Annecke and Doutt 1961: 37; Bouček 1974: 252; Graham 1982: 204.

Type-species: *Flabrinus fabarius* Rondani, by monotypy. Type specimen: lectotype ♀ (MZUF) designated by Bouček (1974) [examined]. Synonymized under *Anaphes* by Bouček (1974: 248). Member of *crassicornis* group.

Anaphoidea Girault 1909: 167; Girault 1910: 246; Gahan 1927: 31; Girault 1929: 11; Kryger 1934: 507; Ogloblin 1939: 144; Doutt 1949: 155; Soyka 1946a: 41; Soyka 1955: 460.

Type-species: *Anaphoidea sordidata* Girault, by original designation. Type specimen: holotype ♀ (INHS) [examined]. Synonymized under *Patasson* by Kryger (1934: 84). Member of *crassicornis* group.

Clinomymar Kieffer 1913: 100; Gahan and Fagan 1923: 36; Debauche 1949: 64 (as *Clynomymar*, misspelling).

Type-species: *Clinomymar peyerimhoffi* Kieffer, by monotypy. Type specimens: syntype ♀♀ (?MHNP) [not examined]. Synonymized under *Anaphes* by Debauche (1949: 63). Member of *crassicornis* group.

Yungaburra Girault 1933: 5; Ogloblin 1939: 144; Annecke and Doutt 1961: 22; Soyka 1949: 419.

Type-species: *Anaphoidea nitens* Girault, by original designation. Type specimens: lectotype ♀ Museum of Victoria, Abbotsford designated by Huber and Prinsloo (1990) [photograph examined]. Synonymized (implicitly) under *Patasson* by Annecke and Doutt (1961: 22). Member of *nitens* group.

Mymar sensu Soyka 1946b: 180; Gahan 1949: 204; Soyka 1955: 460, misidentification.

Synanaphes Soyka 1946b: 181; Annecke and Doutt 1961: 19; Graham 1982: 204.

Type-species: *Synanaphes ranalteri* Soyka, by original designation. Type specimen: holotype ♀ (NHMW) [examined]. Synonymized under *Patasson* by Annecke and Doutt (1961: 19). Member of *fuscipennis* group.

Ferrierella Soyka 1946b: 182; Annecke and Doutt 1961: 19; Graham 1982: 204.

Type-species: *Ferrierella neopratensis* Soyka, by original designation. Type specimen: holotype ♀ (NHMW) [examined]. Synonymized (implicitly) under *Anaphes* by Annecke and Doutt (1961: 19). Member of *fuscipennis* group.

Hofenederia Soyka 1946b: 183; Annecke and Doutt 1961: 22; Graham 1982: 204.

Type-species: *Hofenederia pectoralis* Soyka, by original designation. Type specimen: holotype ♀ (NHMW). Synonymized (implicitly) under *Patasson* by Annecke and Doutt (1961: 22). Member of *crassicornis* group.

Fulmekiella Soyka 1946b: 184; Annecke and Doutt 1961: 23; Graham 1982: 204.

Type-species: *Fulmekiella hundsheimensis* Soyka, by original designation. Type specimen: holotype ♀ (NHMW) [examined]. Synonymized (implicitly) under *Patasson* by Annecke and Doutt (1961: 23). Member of *crassicornis* group.

Stammeriella Soyka 1950: 120; Annecke and Doutt 1961: 19; Graham 1982: 204.

Type-species: *Stammeriella wolfsthali* Soyka, by original designation. Type specimen: holotype ♀ (NHMW) [examined]. Synonymized under *Anaphes* by Annecke and Doutt (1961: 19). Member of *crassicornis* group.

Antoniella Soyka, 1950: 121; Annecke and Doutt 1961: 23; Graham 1982: 204.

Type-species: *Antoniella stubaiensis* Soyka, by original designation. Type specimen: holotype ♀ (NHMW) [examined]. Synonymized under *Patasson* by Annecke and Doutt (1961: 21). Member of *crassicornis* group.

Mariella Soyka 1950: 123; Annecke and Doutt 1961: 23; Graham 1982: 204.

Type-species: *Mariella superaddita* Soyka, by original designation. Type specimen: holotype ♀ (NHMW) [examined]. Synonymized under *Patasson* by Annecke and Doutt (1961: 21). Member of *crassicornis* group.

Austranaphes Ogloblin 1962: 49, as subgenus of *Anaphes*.

Type-species: *Anaphes amplipennis* Ogloblin, by original designation. Type specimen: holotype ♀ (MLPA) [not examined]. Member of *amplipennis* group.

The synomyms and subgenera of *Anaphes*, with their type species, are given mostly according to Graham (1982) who discussed one of them (*Panthus*) in detail. Subsequent references, depository (where known) of the primary type specimen(s) for each type species, and method of type fixation are added here, partly following Schauff (1984a). *Anaphoides* Enock (1915: 181)

is a *nomen nudum* with no included species. Kryger (1934: 507; 1950: 86) and Ogloblin (1939: 144) discussed this name. Peck (1951: 414) designated a type species, *Panthus crassicornis* Walker, for *Anaphoides*. *Anaphoides* is not listed in the generic synonymy above because is an unavailable name. Quite possibly, *Anaphoides* was simply an inadvertent misspelling by Enock of *Anaphoidea* Girault.

Some clarification is required here concerning the gender of *Anaphes*. According to article 30(a) of the ICZN Code a Commission ruling on gender of a name must be followed. China (1965) stated that *Anaphes* was neuter and strict interpretation of the ICZN rules would require that this statement be taken as a Commission ruling on the gender of *Anaphes*. However, standard Greek dictionaries list *Anaphes* (ἀναφής), an adjective meaning impalpable as masculine and Appendix D Table 2 Part B nos. 16 and 17 of the Code give examples of the Greek -es ending as masculine. Although no previous worker has explicitly stated that *Anaphes* is masculine, they have implied that it is by selection of specific epithets which have masculine endings [except *A. punctum* (Shaw)]. Therefore, I assume that China's statement was an inadvertent mistake. In the checklist of species (p. 72) I treated *Anaphes* as masculine and changed the specific epithets correspondingly. Because many species of *Anaphes* were originally placed in genera of feminine gender several changes in agreement were required.

Diagnosis. Females. Antenna with 6 funicular articles and club of 1-3 usually tightly appressed articles separated by oblique, sometimes incomplete grooves (Figs. 9-13). Pronotum entire (Figs. 2, 58, 63). Dorsellum distinct, rhomboidal (Figs. 2, 61, 62, 66). Propodeum sharply declivous in lateral view, not in same plane as scutellum (Figs. 63, 69), and with medial longitudinal groove (Figs. 2, 61, 62, 65). Microtrichia of fore wing unevenly distributed behind and just beyond venation, usually with 2 distinct clear spaces anterior to cubital row of microtrichia, these spaces very small or absent in many species from Australian region (Fig. 8). Fore wing with single dorsal seta basal to marginal cilia just beyond apex of frenal fold (Fig. 6). Tarsi with 4 tarsomeres. Metasoma uniformly coloured, its base not lighter than rest of metasoma, and narrowed at junction with mesosoma, with T2 (petiole) very short, ring-like (Figs. 4, 67); posterior margin of T3 often incised medially (Figs. 4, 68). Ovipositor often projected forward beneath mesosoma in a sac-like extension of the metasoma (Figs. 67, 69). Spiracle on T8 present.

Description. Female. Small to medium specimens (body length 370-1075 µm; FWL 360-1600 µm).

Colour. Body uniformly black or dark brown, rarely lighter brown; exceptionally brownish yellow (one Oriental species) or with metallic blue lustre on head and mesosoma (one Australian species). Base of metasoma same colour as remainder of metasoma. Legs and antenna, especially scape and pedicel, often slightly lighter than body, sometimes yellowish. Fore wing margined with narrow dark brown border at least in apical one third of anterior margin and apex; blade often with faint to distinct fairly uniform brown suffusion, often most noticeable basally behind venation and submarginally around remainder of blade, occasionally blade with 3 dark, distinct, cross bands (some Australian species). Hind wing blade, when tinged, uniformly so, or with fine, irregular, transverse translucent lines.

Sculpture. Head, mesosoma, scape and legs with fine and indistinct to relatively coarse and distinct, cellulate to reticulate sculpture (Figs. 51-66).

Head. Face (Figs. 3, 51, 54) flat or slightly uniformly curved, without subantennal sulcus; 1 pair of intertorular setae; 7 pairs of setae on lower face; 2 to 7 anterior supraorbital setae. Torulus much less than own diameter from transverse trabecula. Subocular sulcus absent. Malar area with 2 setae, ventral seta almost on mouth margin and slightly posterior to dorsal seta.

Labrum with 1 seta (Fig. 3). Mandible with 3 teeth (Figs. 55, 56). Vertex (Fig. 53) with 2 pairs of ocellar setae. Stemmaticum absent. Occiput (Fig. 52) entire.

Antenna with 6 funicular articles, and moderately compact club of 1-3 articles separated by complete or incomplete oblique sutures (Figs. 9-13). Radicle short, almost quadrate (Figs. 57, 58, 60). Scape with fine to coarse and more or less distinct transverse or oblique ridges or striations on inner surface (Fig. 58), finer and more longitudinal striations on outer surface (Figs 57, 60). F1 usually much shorter than F2, rarely as long as F2. Club, when entire, with 6 or 8 sensory ridges; when divided into 2 articles, with 2 sensory ridges on first article, and 4 on second; when divided into 3 articles, with 2 sensory ridges on each article. Sensory ridges of flagellomeres usually straight (Figs. 9-11, 13, 37-50) sometimes strongly curved apically (Fig. 12).

Mesosoma. Pronotum entire (Figs. 2, 61, 66). Pronotal spiracle flush with surface, about 2 times diameter of propodeal spiracle. Prosternum divided longitudinally (Fig. 64). Scutellum clearly divided into anterior and posterior parts; anterior scutellum with 1 and 1 setae, and a deep excavation posterolaterally (Figs. 2, 61, 62). Metanotum distinct, with 1 and 1 small setae lateral to dorsellum (Fig. 65); dorsellum rhomboidal, clearly separated from lateral wings of metanotum (Figs. 2, 61, 62, 65). Propodeum sharply declivous (Figs. 63, 69) with a distinct narrow longitudinal groove medially (Figs. 2, 61, 62, 65); propodeal seta usually separated from spiracle by distance shorter than between placoid sensilla of anterior scutellum (at most about 2 times diameter of propodeal spiracle). Second phragma usually weakly truncated posteriorly, sometimes slightly notched apically; at most projecting into metasoma to posterior margin of T2 (Fig. 2).

Wings. Macropterous, rarely brachypterous. Fore wing very narrow (Fig. 7) to very wide (Fig. 8) (FWL/FWW 15.7-2.2), with asymmetrical rhomboidal apex (sometimes very slight asymmetry) in which the curved apical portion of anterior margin is somewhat longer than corresponding portion of posterior margin (Figs. 7, 8, 20-36). Microtrichia of blade distributed evenly beyond venation except for marginal and medial spaces, microtrichia usually numerous on dorsal surface of marginal vein; cubital row complete, extending to base of marginal vein and often beyond (Fig. 6). Marginal and medial spaces almost absent in many Australian species (Fig. 8). One, or rarely two, setae on ventral surface of blade membrane at about level of apex of submarginal vein. Apex of frenal fold basal to marginal cilia with a distinct dorsal seta projecting posteriorly (Fig. 6). Submarginal vein with bullae apically, and 1 basal macrochaeta. Marginal vein with proximal macrochaeta subequal in length to distal macrochaeta, 0-2 marginal microchaeta between macrochaetae; hypochaeta distal to proximal macrochaeta (Fig. 6). Stigmal vein about 0.4-0.6 times length of marginal vein. Hind wing linear, often distinctly curved, with 1 anterior and 1 posterior row of submarginal microtrichia and few to many microtrichia apically on disc between these rows.

Legs. Fore tibia with up to 13 conical sensilla in 2 rows on anteroventral surface. Tarsi with 4 tarsomeres, first tarsomere of middle and hind legs as long as or longer than second tarsomere.

Metasoma. Metasoma with only 6 terga (T3-T8) conspicuous; T2 very short, ring-like, not usually visible except in slide-mounts (Figs. 4, 67); posterior margin of T3 usually incised (Figs. 4, 62, 68); T8 with spiracle (Figs. 67-70). Ovipositor and sterna basally often extended anteriorly between coxae, occasionally as far as head, apex not or very slightly exserted beyond apex of metasoma (Figs. 69, 70). Cercus with 4 setae.

Male. Antenna with 11 flagellomeres (Fig. 15); in *Anaphes s.s* and three species of *A.* (*Yungaburra*) F1 greatly reduced (wider than long) (Figs. 16-18, 59) so antenna apparently with only 10 flagellomeres (Fig. 14); each flagellomere with 4 (basal flagellomeres) to about 7 (apical flagellomeres) sensory ridges except for F1 in *Anaphes s.s.* (with 0 sensory ridges) and three

species of *A.* (*Yungaburra*) (with 1 sensory ridge). T8 without spiracle. Male genitalia completely exposed ventrally, not covered by sternites, with long parameres (Figs. 73-76).

Key to subgenera and species groups of *Anaphes*.

1 Flagellum of antenna with 11, or apparently 10, flagellomeres and without club; males 2
- Flagellum of antenna with 6 funicular articles and distinct club of 1-3 articles; females 3

2(1) Antenna apparently with 10 flagellomeres (Fig. 14) each bearing several sensory ridges, F1 small (wider than long), without sensory ridges (Figs. 16, 17). Worldwide. . . . . *A.* (*Anaphes*) (*fuscipennis* and *crassicornis* groups)
- Antenna with 11 flagellomeres, if apparently with 10 flagellomeres then F1 small (wider than long), with 1 transverse sensory ridge (Figs. 18, 59). Southern Neotropical, Australian, and southeastern Oriental regions . . . . . *A.* (*Yungaburra*) (*nitens* and *amplipennis* groups, and an unnamed group)

3(1) Club with 6 sensory ridges 4
- Club with 8 sensory ridges 6

4(3) Club entire . . . . . *fuscipennis* group
- Club partly or completely divided into 2 articles 5

5(4) Fore wing with marginal and medial spaces very small or absent; parasites of *Gonipterus* spp. (Curculionidae) . . . . . *nitens* group (part)
- Fore wing with distinct marginal and medial spaces; parasites mostly of Chrysomelidae or Curculionidae other than *Gonipterus* spp., sometimes parasites of other families . . . . . *crassicornis* group

6(3) Club entire . . . . . *amplipennis* group
- Club partly or completely divided into 2 or 3 articles 7

7(6) Club partially or completely divided into 2 articles . . . . . *nitens* group (part)
- Club partially or completely divided into 3 articles . . . . . unnamed group

Review of the described Nearctic species of the *fuscipennis group*.

Nine described species are reviewed, a reduction from the twelve listed in Burks (1979). One of the species listed therein, *A. pallipes* (Ashmead), is here transferred to the *crassicornis* group, and three were synomymized by Huber and Rajakulendran (1988). One new species is described below. Many more exist but are not described here, for reasons given above. No species of the *fuscipennis* group have been described from south of the USA so this review is, in effect, for all the described western hemisphere species.

The number of valid names in *A.* (*Anaphes*) greatly exceeds the number of valid species because of the work of W. Soyka in Europe. The number of valid species in *A.* (*Anaphes*) will undoubtedly be reduced through synonymy. This number will probably only partially be compensated by description of new species from all regions.

Key to described North American species of the *fuscipennis* group.

Females

1. F4 without sensory ridges (Figs. 9, 37) 2
- F4 with 1 or 2 sensory ridges 3

2(1) Fore wing very narrow, FWL/FWW greater than 9.5, hind margin slightly concave (Fig. 20); hind tarsomere 1 subequal to tarsomere 2 . . . . . *A. sinipennis* Girault (p. 37)
- Fore wing much wider, FWL/FWW less than 5.2, hind margin straight or slightly convex (Fig. 21); hind tarsomere 1 at least 1.6x as long as tarsomere 2 . . . . . *A. fuscipennis* Haliday (p. 38)

3(1) Head with occipital suture on each side converging medially toward and almost reaching foramen magnum (Figs. 5, 6 in Huber and Rajakulendran 1988); fore wing with posterior margin hyaline except at apex . . . . . *A. iole* Girault (p. 41)
- Head with occipital suture on each side not converging medially, more or less parallel to margin of compound eye (e.g. Fig. 52); fore wing with posterior margin usually narrowly rimmed with brown for much of its length 4

4(3) F4 with 1 sensory ridge 5
- F4 with 2 sensory ridges 6

5(4) F2 at least 4.7 times as long as wide (Fig. 38) . . . . . *A. byrrhidiphagus* n.sp. (p. 43)
- F2 at most 2.7 time as long as wide . . . . . *A. alaskae* Annecke and Doutt (p. 44)

6(4) F2 usually with 1, rarely 2, sensory ridges 7
- F2 without sensory ridges 8

7(6) Smaller species (FWL less than 780µm); FWL/FWW greater than 6.0 . . . . . *A. nigrellus* Girault (p. 45)
Larger species (FWL about 840µm); FWL/FWW less than 5.7 . . . . . *A. hercules* Girault (p. 47)

8(6) Host: *Oulema melanopus* (Chrysomelidae) . . . . . *flavipes* Förster (p. 47)
- Host: *Dibolia borealis* (Chrysomelidae) . . . . . *behmani* Girault (p. 50)

Anaphes sinipennis Girault
(Figs. 20, 37)

Anaphes sinipennis Girault 1911c: 187 (***nomen nudum***); Girault 1911e: 280; Girault 1912b: 153; Girault 1913: 117; Girault 1929: 13; Burks 1979: 1029; Schauff 1984a: 48.
Mymar sinipennis; Peck 1951: 416; Peck 1963: 41.

Type material. SYNTYPES ♀♀ (INHS) [not examined]. I could not locate the type specimens and they have evidently been missing for many years because neither Frison (1927) nor Webb (1980) listed them. Girault (1911e) designated two of the three original specimens as types but did not designate a holotype. There are two female specimens in the USNM identified as *A. sinipennis* by Girault. Neither belongs to the type series. They were collected in the type locality (Urbana, IL) on 14.VIII.1901 on a greenhouse window by Girault, and 20.V.1911 on a window by Williamson and Girault, respectively. Both specimens agree very well with the original description and can serve as reference specimens. A neotype is not designated for this distinctive species.

Diagnosis. Female. Differs from all other North American *Anaphes* by the following combination of attributes: F1-F4 without sensory ridges, F5 with 1, and F6 with 2 ridges; club slightly wider apically than basally, often almost truncate apically, and very wide relative to F6 (Fig. 37); fore wing (Fig. 20) very narrow (FWL/FWW 9.6-10.8) and distinctly curved apically and hind margin of fore wing distinctly concave. *A. sinipennis* is very similar to *A. fuscipennis* in antennal structure.

Description. Female. Colour. Body uniformly dark brown. Fore wing distinctly tinged with brown behind venation, especially behind stigmal vein and apex of marginal vein, and in marginal space; posterior margin entirely rimmed with brown. Hind wing uniformly tinged with brown.

Body length. $\bar{x}$=591 (496-880, n=9).

Head. Head width 213 (200-230, n=10); occipital suture represented by very short line almost parallel to posterior orbit, extending to level well above dorsal margin of foramen magnum. Length of antennal articles (n=10): radicle+scape 143 (132-165); pedicel 60 (54-67); F1-F6 27 (23-31), 48 (38-56), 46 (40-55), 44 (40-51), 47 (40-55), 53 (47-60); club 130 (121-143). F1-F4 narrower than F5 and F6 and without sensory ridges, F5 with 1 and F6 with 2 ridges; club often slightly wider apically than basally, and truncated apically (Fig. 37).

Mesosoma. Mesoscutum width 168 (148-173, n=7).

Wings. Fore wing length 716 (625-804, n=11), width 70 (58-86), posterior margin concave (Fig. 20); length of marginal space 148 (129-176); FWW/FWL 10.25 (9.6-10.8); LMC 160 (139-173) about 2.3 times wing width. Hind wing length 703 (615-783), width 23 (19-29); LMC/HWW about 5.4.

Metasoma. Ovipositor length 248 (227-290, n=8), about 1.0 times hind tibial length, extending anteriorly at most to base of hind coxa

Male. Similar to female. Length of antennal articles (excluding F1 which is minute) (n=1): radicle+scape - ; pedicel 49; F2-F11 67, 76, 78, 76, 76, 75, 81, 80, 78, 67.

Distribution. North America.

Material examined. 41♀♀ and 1♂ (23 on slides).

CANADA. **Alberta**. Wagner Natural Area, 6 km W. Edmonton, 6-13.VIII, 13-22.VIII, 28.VIII-10.IX.1985, A. Finnamore and T. Thormin (24♀♀ and 1♂, PMAE, CNCI). **Nova Scotia.** S. Harbour, 60º67'W, 46º52'N, 28-31.V.1983 (1♀, CNCI). **Ontario.** London, Fanshawe experimental farm, 1-31.IX.1982, A. Tomlin (1♀, CNCI); Ottawa, 2-14.IX.1991, J.R. Vockeroth (1♀, CNCI), Mer Bleue, 16-23.VIII.1982, H. Goulet (1♀, CNCI); Oxford Mills, 22-25.V, 25-28.V,

29.V-1.VI, and 1-5.VI.1973, L. Masner (10♀♀, CNCI). **Québec.** Gatineau Park, Camp Fortune, 1-14.VI.1983, J. Denis (1♀, CNCI).

U.S.A. **California**. *Tulare Co.*: Ash Mountain Power Station # 3, 26.VI.1983, J.A. Halstead (1♀, CNCI). **Florida**. *Manatee Co.*: Bradenton, 1-7.IV.1986, D.J. Schuster (1♀, CNCI). **Illinois.** *Champaign Co.*: Urbana, 20.V.1911, Williamson and A.A. Girault (1♀, USNM), 14.VIII.1901, A.A. Girault (1♀, USNM). **Maryland**. *Prince George's Co.*: Patuxent Wildlife Research Center, 22-25.VI.1980, L. Masner (1♀, CNCI).

Hosts and Biology. Unknown. *A. sinipennis* is found mostly in riparian habitats. A specimen from Ottawa was collected by sweeping *Sagittaria*. One from London was collected in an onion field.

Comments. Although the type series is missing, the detailed original description and the existence of two specimens determined by Girault (USNM) permits the species to be recognized. The paper by Girault (1911c) in which the specific epithet *sinipennis* was mentioned precedes the formal description of the species (Girault 1911e) by about 1 month.

Anaphes fuscipennis Haliday
(Figs. 2, 6, 9, 17, 21)

Anaphes fuscipennis Haliday 1833: 346; Walker 1846: 51; Förster 1847: 213; Loew 1847: 342; Lubbock 1863: 2; Kirchner 1867: 202; Ashmead 1904: 363; Schmiedeknecht 1909: 499; Gahan and Fagan 1923: 12; Kloet and Hincks 1945: 304; Soyka 1946b: 180; Debauche 1948: 159; Debauche 1949: 64; Gahan 1949: 204; Kryger 1950: 9; Soyka 1955: 461; Annecke and Doutt 1961: 19; Tudor and Boţoc 1975: 179; Fitton *et al.* 1978: 110; Trjapitzin 1978: 528; Graham 1982: 206; Schauff 1984a: 48; Huber 1986: 197; Trjapitzin 1987: 963.

Mymar fuscipennis; Soyka 1949: 310.

Anagrus fuscipennis; Blanchard 1840: 293.

Anaphes pratensis Förster 1847: 211; Loew 1847: 342; Kirchner 1867: 202; Ashmead 1897: 138; Dalla Torre 1898: 424; Lameere 1907: 247; de Gaulle 1908: 110; Schmiedeknecht 1909: 499; Girault 1911b: 135; Girault 1911c: 188; Girault 1911d: 364; Girault 1912a: 88; Girault 1912c: 299; Girault 1914: 110; Britton 1920: 323; Howard 1927: 14; Christie 1929: 43; Girault 1929: 14; Pack and Fife 1930: 30; Couturier 1935: 89; Feytaud 1937: 66; Soyka 1946a: 40; Debauche 1948: 163; Hamlin *et al.* 1949: 58; Soyka 1949: 310; Thompson 1958: 568; Hincks 1960: 213; Boţoc 1962: 111; Bakkendorf 1964: 4; Brunson and Coles 1968: 6; Tudor and Boţoc 1975: 180; Aeschlimann 1975: 405; Aeschlimann 1977: 111; Clausen 1978: 267; Fitton *et al.* 1978: 110; Trjapitzin 1978: 528; Burks 1979: 1029; Aeschlimann 1980: 145; Schaber 1981: 169; Graham 1982: 206; Collins and Grafius 1983: 2; Huber 1986: 197; Trjapitzin 1987: 963.

Mymar pratensis; Peck 1951: 416; Clausen 1956: 116; Peck 1963: 41.

Ferrierella pratensis; Soyka 1949: 347.

Ferrierella capitulata Soyka 1949: 341. **Syn. n.**

Ferrierella filicornis Soyka 1949: 343. **Syn. n.**

Ferrierella maculata Soyka 1949: 345. **Syn. n.**

Ferrierella neopratensis Soyka 1946b: 182; Soyka 1949: 338; Schauff 1984a: 47. **Syn. n.**

Ferrierella stammeri Soyka 1949: 349. **Syn. n.**

Type material. ***Anaphes fuscipennis***. LECTOTYPE ♀ (NMID) [examined]. On card labelled: 1."37.XX"[blue label]. 2."British Haliday 20.2.82." 3."*fuscipennis*.". 4."*Anaphes fuscipennis*

Haliday LECTOTYPE: ♀ M. de V. Graham det. 1972". The lectotype is in good condition, mounted dorsal side up and slightly on its left side. PARALECTOTYPES were designated and discussed by Graham (1982). I examined 1 male in good condition on a card point, which was collected on the same date as the lectotype.

Anaphes pratensis. LECTOTYPE ♀ (NHMW), here designated. On slide labelled: 1."*An. pratensis* Förster, Type. 2."Collect. G. Mayr". 3."61". 4."In Canadab. 1944". 5."Co-Type". 6."*Ferrierella* ♀ *pratensis* Förster Type dt. Soyka". 7."LECTOTYPE *Anaphes pratensis* Förster ♀ des. Huber 1987". The lectotype is in reasonable condition, mounted laterally. PARALECTOTYPES, here designated: 3♂♂, same data (handwritten by Soyka) as lectotype but numbered "62", "63", and "64", respectively. They are dirty and in rather poor condition.

Förster (1847) did not state how many specimens of *A. pratensis* he had. Soyka (1949) found a female on a minuten pin in Mayr's collection which he slide mounted. He also slide-mounted 3 males, evidently from the same pinned series, which he did not directly mention in his redescription. Soyka labelled Förster's female specimen as co-type, although in his description he referred to it as "type". He then incorrectly labelled as "type" a specimen (no. 891) that he himself had collected in 1934. Soyka (1949) stated that males were doubtfully known ("noch unsicher") presumably referring to the male specimens from Mayr's collection that he had slide mounted. I agree with him regarding these 3 males. None of them are conspecific with the lectotype because the relative proportions of tarsomere 1 and 2 are not those of *A. fuscipennis*. I do not know to which species they belong but they undoubtedly belong to the original syntypical series so I labelled them as paralectotypes.

Anaphes capitulata. HOLOTYPE ♀ (NHMW). On slide labelled: 1."*Ferrierella* ♀ *capitulata* Soyka Type". 2."Type". 3."864". 4."Valkenburg, Holland IgnatiusKolleg am fenster 31. Juni 1931 lg Soyka In Canadab. 1941". The holotype is in good condition, mounted laterally.

Anaphes filicornis. HOLOTYPE ♀ (NHMW). On slide labelled: 1."*Ferrierella* ♀ *filicornis* Soyka Type". 2."Type". 3."873". 4."Valkenburg-Holland Ignat.-Koll. am fenster 31.Juni 1931 - lg Soyka Coll. Soyka In Canadab.". The holotype is in good condition, mounted laterally.

Ferrierella maculata. HOLOTYPE ♀ (NHMW). On slide labelled: 1."*Ferrierella* ♀ *maculata* Soyka Type". 2."Type". 3."877". 4."Valkenburg Holland Ignatiuskolleg am fenster 18 Juni 1931 lg [something illegible] det W. Soyka In Canadab. 1941". The holotype is in good condition, mounted laterally with head detached and face down.

Ferrierella neopratensis. HOLOTYPE ♀ (NHMW). On slide labelled: 1."*Ferrierella neopratensis* Soyka ♀ Geno-Type". 2."G.Type". 3."881". 4."Hundsheim-SpitzerBerg Südseite 2 Sept. 1941 lg Novicky [something illegible] et det W. Soyka In Canadab. 1941". The holotype is in good condition, mounted laterally.

Ferrierella stammeri. HOLOTYPE ♀ (NHMW). On slide labelled: 1."*Ferrierella* ♀ *stammeri* Soyka Type". 2."Type". 3."901". 4."Breslau-Grüneiche D'land - 24.IX.1933 lg. Stammer In Canadab.". The holotype is in poor condition (head, 1 fore wing, 1 hind wing and 1 antenna beyond scape detached) and poorly oriented near edge of cover slip.

Diagnosis. Female. Differs from all other North American *Anaphes* by the following combination of attributes: F1-F4 of antenna distinctly narrower than F5 and F6, and without sensory ridges (Fig. 9); fore wing with hind margin straight or slightly convex; tarsomere 1 of hind leg at least 1.6 times as long as tarsomere 2 (subequal in other species).

Description. Female. Colour. Dark brown. Fore wing with some infuscation behind venation and narrowly along posterior margin for short distance beyond frenal fold.

Body length. $\bar{x}$=693 (471-923, n=10).

Head. Head width 298 (266-329, n=8); occipital suture represented by short line almost parallel to posterior orbit, extending ventrally to level of dorsal margin of foramen magnum. Length of antennal articles (n=10): radicle+scape 138 (118-164); pedicel 64 (57-64); F1-F6 33 (29-38), 98 (84-118), 89 (68-109), 78 (65-94), 73 (59-87), 72 (63-84); club 143 (132-156). F1-F4 distinctly narrower than F5 and F6 and without sensory ridges, F5 with 1 and F6 with 2 sensory ridges (Fig. 9).

Mesosoma. Mesoscutum width 246 (228-269, n=5).

Wings. Fore wing length 900 (766-1069, n=9), width 191 (141-257), posterior margin straight or slightly convex (Fig. 21); length of marginal space 152 (131-203); FWW/FWL about 4.8 (4.16-5.13); LMC 173 (151-195), about 0.9 times wing width. Hind wing length 871 (739-1057), width 43 (35-60); LMC 150 (121-191); LMC/HWW about 3.5.

Metasoma. Ovipositor length 474 (442-529, n=8), about 1.5 times hind tibial length, extending anteriorly at most to base of hind coxa.

Male. Similar to female. Length of antennal articles (excluding F1 which is minute) (n=3): radicle+scape 103 (96-118); pedicel 48 (45-54); F2-F11 69 (61-78), 74 (68-87), 72 (64-84), 71 (66-78), 68 (64-76), 69 (66-74), 70 (65-74), 72 (68-79), 69 (66-74), 76.

Distribution. Europe, Algeria, Israel, North America. North American specimens examined were collected from March to August, October and November. European specimens examined were collected from January to February and in May. Schaber (1981) summarized the distribution of *A. fuscipennis* in N. America. I include only specimens that I have examined in the distribution list below.

Material examined. 80♀♀ and 16♂♂ (23 on slides).

ALGERIA: Atlas de Blida, Chréa sur Blida, 1400m, 3.v.1988, C. Besuchet, I. Löbl and D. Burkhardt (1♀, MHNG); Oran, bord de route D75, 27.XII.1958, J. Barbier (1♀, CNCI).

CANADA. **British Columbia.** Burnaby Mt., 14-18.IV.1980, D.G. Gillespie (1♀, CNCI); Sidney, 1-28.IV.1986, D.G. Gillespie (6♀♀ and 4♂, CNCI), Summerland, 5.V.1959, R.E. Leech (1♀, CNCI). **Nova Scotia.** Cape Breton Highlands National Park, Chéticamp, 31.V.1984 (2♀♀, CNCI), Chéticamp river, 28.V, 30.V, and 1.VI.1984, H. Goulet (3♀♀ and 1♂, CNCI), MacKenzies Peak, 11.VII.1983, J.R. Vockeroth (1♀, CNCI). **Ontario.** Almonte, 3-12.V.1986, H. Goulet and L. Dumouchel (2♀♀, CNCI); 7 mi. w. Carleton Place, 20-25.VI.1980, S.J. Miller (1♀, CNCI); Chatterton, 13 mi N. Belleville, 29.V.1967, 8.IV. 18.V. and 30.X.1968, C.D. Dondale (8♀♀, CNCI); Gloucester, 4-17.X.1984, M. Sanborne (1♀, CNCI); London, Fanshawe experimental farm, 5.XI.1982, A. Tomlin (1♀, CNCI); Owen Sound, 22.V.1978, J.M. Cumming (2♀♀, CNCI); Shirley's Bay, Innes Point, 3-10.X.1985, J. Denis (1♀, CNCI). **Quebec.** Gatineau Park, Ridge Road, 9.V.1986, S.B. Peck (4♀♀, CNCI), Luskville Falls, 300m, 9-21.V.1986, J. Denis and L. Dumouchel (4♀♀, CNCI).

ISRAEL. Galilee, Eilon, N. Betzet, 20.IV.1982, C. Besuchet and I. Löbl (3♀♀, MHNG).

U.S.A. **California**. *Contra Costa Co.*: El Cerrito, 6.III.1948, R.L. Doutt (1♀, USNM). **Connecticut.** *New Haven Co.*: New Haven, 10.V.1904, H.L. Viereck (1♀ and 1♂, USNM). **Delaware**. *Kent Co.*: Smyrna, 8.III.1972, D.W. Angalet (2♀♀, USNM). **Idaho.** *Shoshone Co.*: Hobo Cedar Gr. 15.VII-23.VIII.1985 (1♀, UICM). **Illinois.** *Champaign Co.*: Urbana, 7.V.1911, A.A. Girault (1♀, USNM). **Michigan**. *Berrien Co.*: Niles, 13.V.1969, T.R. Burger (1♀, USNM). **New York**. *Tompkins Co.*: Ithaca, V.1924, H.J. Pack (5♀♀, USNM). **Oregon**. *Jackson Co.*: Medford, J.C. Hamlin (6♀♀ and 1♂, USNM). **Utah**. *Salt Lake Co.*: Salt Lake City, 25.III, and 10.V.1926, T.R. Chamberlin (5♀♀, USNM), 9.VI.1911, T.H.Parks (1♀, USNM). **Wisconsin**. *Columbia Co.*: Ray Geyman farm, 10 mi. E. Baraboo, fall.1984, W. Gould (4♀♀, CNCI); *Dane Co.*: Madison, V.1985, W. Gould (10♀♀ and 9♂♂, CNCI).

Hosts and Biology. Curculionidae: *Sitona humeralis* Stephens (Aeschlimann 1977), *Hypera postica* (Gyll.), and *H. punctata* (Fabr.) (Clausen 1956). Ashmead (1897) recorded *Cecidomyia avenae* March. (Cecidomyiidae) as a host but this has never been corroborated and it is probably incorrect. Couturier (1935) and Feytaud (1937) recorded unsuccessful attempts by *A. fuscipennis* to parasitize eggs of *Leptinotarsa decemlineata* (Say). If this mymarid identification is correct (voucher material was not studied), then this demonstrates the opportunistic nature of mymarids, in that unsuitable, unrelated, hosts may be attacked. An interesting note is that the five specimens from Ithaca, New York, were collected from the stomach of a trout.

Comments. Because of its potential as a biological control agent there is a considerable literature, including at least one thesis (Gould 1986) referring to *A. fuscipennis*. This species of European origin was probably introduced into North America together with *A. luna* beginning in 1911 (Clausen 1956, 1978). At the time of introduction, and for many years after, the two species were confused so that earlier references (before about 1950) to one or the other species may have referred to both. The female antenna figured in Chamberlin (1924) is almost certainly that of *A fuscipennis* rather than *A. luna*. Thus, early references to *A. luna* in N. America, as summarized under *Mymar pratensis* by Peck (1963) and discussed by Schaber (1981) evidently referred, at least in part, to *A. fuscipennis* (as *A. pratensis*). Those references that specifically mention *A. pratensis* are included above.

If *A. fuscipennis* had become established upon its original release in May-June, 1911, in Utah then it would have had to spread exceedingly rapidly on its own to Urbana, Illinois, where Girault collected one specimen in May, 1911. But, in fact, the species (under the name *A. luna*) did not become established at that time (Chamberlin 1924). Therefore, *A. fuscipennis* already occurred in N. America, perhaps as a previous accidental introduction, but went unrecognized until field-collected eggs of its hosts were reared for parasites.

Graham (1982) stated that *Anaphes fuscipennis sensu* Debauche (1948) is certainly not *A. fuscipennis*. I examined Debauche's specimens and conclude that they are the same as *A. medius* (Soyka). Hellén's (1974: 25) redescription of *A. fuscipennis* applies to another species, not *A. fuscipennis*. The record by Varis (1972: 22), quoted by CIBC (1979: 4), of *A. fuscipennis* reared from *Lygus* is probably the same species as *A. fuscipennis sensu* Hellén. The reference to *A. fuscipennis* by Bouček (1974: 248) probably also refers to a species other than *A. fuscipennis*.

Anaphes iole Girault

(Figs. 54, 60, 64, 68, 70, 72, 73-76)

Anaphes iole Girault 1911b: 135 (*nomen nudum*); Girault 1911c, 188 (*nomen nudum*); Girault 1911e: 284; Girault 1912a: 89; Girault 1916: 6; Girault 1929: 13; Thompson 1958: 568; Burks 1967: 215: Burks 1979: 1029; Schauff 1984a: 48; Huber and Rajakulendran 1988: 894; Sohati *et al.* 1989: 1127; Cohen *et al.* 1989: 15; Jones and Jackson 1990: 463.

Mymar iole; Soyka 1949: 331; Peck 1951: 416; Peck 1963: 39.

Anaphes iole anomocerus Girault 1929: 13; Huber and Rajakulendran 1988: 894.

Mymar iole anomocerus; Soyka 1949: 331.

Anaphes anomocerus; Strong 1936: 66; Strong 1937: 57; Strong 1938: 52; Ewing and Crawford 1939: 303; Thompson 1958: 568; Burks 1979: 1029; Rajakulendran and Cate 1986: 255; Strand 1986: 107.

Mymar anomocerus; Peck 1951: 416; Peck 1963: 38.

Anagrus ovijentatus Crosby and Leonard 1914a: 181; Crosby and Leonard 1914b: 483; Gahan *et al.* 1928: 984; Glick 1939: 48; Hoebeke 1980: 20.

Anagrus ovijententatus; Bakkendorf 1926: 270 (= *Anaphes*). Incorrect subsequent spelling.

Anaphes ovijentatus; Girault 1929: 14; Romney and Cassidy 1945: 497; Clancy and Pierce 1966: 854; Stoner and Surber 1969: 501; Stoner and Surber 1971: 1566; Varis 1972: 22; Scales 1973: 305; Sillings and Broersma 1974: 124; Burks 1979: 1029; CIBC 1979: 4; Graham and Jackson 1982: 56; Jackson and Graham 1983: 772; Collins and Grafius 1983: 2; Jackson and Cohen 1984: 437; Graham *et al.* 1984: 250; Graham *et al.* 1986: 138; Jackson 1986: 149; Strand 1986: 107; Jackson 1987: 367; Jackson and Debolt 1987: 10; Gordon *et al.* 1987: 347; Driesche and Hauschild 1987: 27; Debolt 1987: 82; Huber and Rajakulendran 1988: 894; Jackson *et al.* 1988: 919.

Mymar ovijentatus; Soyka 1949: 332; Peck 1951: 416; Peck 1963: 39; Stoner and Surber 1969: 501.

Anaphes perdubius Girault 1916: 6; Beyer 1921: 24; Girault 1929: 14; Couturier 1935: 92; Thompson 1958: 568; Burks 1979: 1029; Huber and Rajakulendran 1988: 894.

Mymar perdubius; Soyka 1949: 332; Peck 1951: 416; Peck 1963: 40.

Type Material. ***Anaphes iole.*** HOLOTYPE ♀ (INHS) [not examined]. Girault described *A. iole* from a single female specimen. The type is no longer in the INHS and has been missing for many years because neither Frison (1927) nor Webb (1980) mentioned it.

Anaphes ovijentatus. LECTOTYPE ♀ (CUIC), here designated. On slide labelled: 1."No. HOLOTYPE *Anagrus ovijentatus* Crosby and Leonard Date Oct. 7, 1913 Ithaca, N.Y.". 2."HOLOTYPE Cornell U. No. 42.1". 3."LECTOTYPE *Anagrus ovijentatus* Crosby and Leonard ♀ des. Huber 1987". The lectotype is in good condition, mounted laterally with head detached and face up. PARALECTOTYPE, here designated: 1♀ in a microvial in alcohol, in very poor condition (only part of mesosoma and legs remaining). Crosby and Leonard (1914a) described *ovijentatus* from three females. Only two females were found. Hoebeke (1980) incorrectly stated that the type series consisted of a holotype and two paratypes, but because Crosby and Leonard (1914a) did not designate a holotype in the description a lectotype is designated here.

Anaphes anomocerus. LECTOTYPE ♀ (USNM), here designated. On slide labelled: 1."*Anaphes perdubius* Girault ♂ ♀ *anomocerus* Gir. *anomocerus* Type No. 20966 U.S.N.M.". 2."Webster No. 16806 *Anaphes perdubius* Gay. Ga. 9-9-1916 *anomocerus* Gir. Egg parasite *H. citri* on alfalfa ♂ ♀ types. A.H. Beyer". 3."LECTOTYPE *Anaphes anomocerus* Girault des. Huber 1987". The lectotype is in good condition, mounted on its left side.

The only description of *A. anomocerus* occurs in a key (Girault 1929) with no indication of how many specimens had been examined, or what the collection data was. The collection data is given on the type slides and is also entered in the type book at the U.S. National Museum (as *Anaphes perdubius anomocerus*). I examined six specimens on two slides. The lectotype slide bears, under a single badly crushed coverslip, two dark coloured *A. anomocerus* male and female positioned one on top of the other, one light coloured *anomocerus* female, and three females of *Anagrus* sp. The light coloured *anomocerus* is designated as lectotype. It is poorly positioned alone near the edge of the coverslip. PARALECTOTYPES, here designated: 1♀ and 1♂ *A. anomocerus* on the lectotype slide and the 3♂♂ *A. anomocerus* on the second slide, all under one coverslip with three *Anagrus* sp.

Anaphes perdubius. HOLOTYPE ♀ (USNM). On slide labelled: 1."*perdubius* 19186". 2."Webster No. 8827 *Anaphes perdubius* Gir. Salt Lake City Utah Sept. 2 1912 reared from Jassid eggs *Anagrus nigriventris* C.N. Ainslie Collector". The holotype is in reasonably good condition, with left antenna and right hind wing missing, metasoma broken off and mounted laterally, head broken off and mounted face up, mesosoma mounted dorsolaterally with wings outstretched.

Diagnosis. Female. Differs from all other North American *Anaphes* by the following combination of attributes: head with occipital suture converging to foramen magnum; dorsal surface of fore-wing blade with posterior row of microtrichia usually separated from hind margin by a distinct gap of about 1 microtrichia length; posterior margin of fore wing hyaline except for apex; mesosoma relatively long compared to metasoma.
Description. The species was redescribed by Huber and Rajakulendran (1988).
Comments. The importance of *A. iole* as a potential biological control agent of species of *Lygus* and *Pseudatomoscelis* has resulted in a considerable literature and at least two theses (Jackson 1982; Rajakulendran 1986). The two papers by Girault (1911b,c) in which the specific epithet *iole* was mentioned precede the formal description of the species (Girault 1911e) by about 1 month.

Anaphes byrrhidiphagus Huber sp.n.
(Figs. 4, 5, 22, 38)

Type material. HOLOTYPE ♀ (USNM): on slide under 3 cover slips, labelled: 1."OR. Benton Co. Mary's Peak n. side 27-III-77 P.J. Johnson ex. egg *Lioligus nitidus* in moss". 2."*Anaphes byrrhidiphagus* Huber ♀ HOLOTYPE U.S.N.M. Type no. 104415." In good condition, dissected and mounted under 4 cover slips. ALLOTYPE ♀ (USNM), same locality as holotype, ex. *Lioon* sp. PARATYPES. 88♀♀ and 20♂♂, all in CNCI unless otherwise noted. CANADA. **British Columbia.** East Sooke Pk, 12-24.IX.1984, R.A. Cannings (1♀ on point); Queen Charlotte Islands, Graham Island, Tow Hill, 7.VII.1983, I.M. Smith (1♀ on point); Queen Charlotte Islands, Graham Island, Massett Beach nr. Chown River, 9-13.VII.1983, I.M. Smith (1♀ on point); Smithers, Hudson Bay Mtn, 20.VII.1983, J.D. Smith (2♀♀ on slide and point); Terrace, 5.VIII.1960, W.R. Richards (1♀ on point); Vancouver Island, Lake Cowichan, 19-28.VII.1985, I.M. Smith (1♂ and 2♀♀ on points); Vancouver, Point Grey, IV.1975, J.R. Vockeroth (1♀ on point). **Manitoba.** Churchill, 9.VIII.1952, J.G. Chilcott (1♀ on slide, CNCI). **Quebec.** Chimo, 17-18.VIII.1959, W.R.M. Mason (2♀♀ on slides CNCI); Great Whale River, 8.VIII.1959, W.R.M. Mason (1♀, CNCI). USA. **Alaska and Yukon**. Chicken to Dawson, 16.VIII.1984, S.and J. Peck, car net (1♀ on point). **Idaho.** *Idaho Co.*, 10 mi. E. Slate Creek, 22.VI.1984 (1♀ and 3♂♂, UICM); 22 mi. ESE. Lowell, 25.VIII.1985, T.D. Miller (1♀, UICM); *Shoshone Co.*, Hobo Cedar Gr., 15.VII-23.VIII.1985, T.D. Miller (3♀♀ and 1♂, UICM). **Oregon**. *Benton Co.*, Philomath, Mary's Peak, Parker Creek, 14.VII.1985, I.M. Smith (10♀♀ and 1♂ on slides, 21♀♀ and 4♂♂ on points); *Benton Co.*, Philomath, Mary's Peak, along Parker Creek, 4000', 28.VI.1983, I.M. Smith (1♀ on point); *Curry Co.*, Port Oxford, 10.VII.1985, I.M. Smith, stream by road to Gribble Campground (3♀♀ on points); *Lane Co.*, Deadwood Creek, 18.VIII.1982, J.B. Woolley (3♀♀ and 2♂♂ on points). **Washington.** *Jefferson Co.*, Olympic National Park, Quinault Rain Forest, 19 mi. E. Quinault, 13.VIII.1985, A. Finnamore, T. Thormin (4♀♀ on points); *Pierce Co.*, Mt. Rainier National Park, Sunshine Point Campground, 11.VII.1985, A. Finnamore, T. Thormin (1♀ on point); Mt. Rainier National Park, Longmire Marsh, 1000m, 29.VII.1985, L. Masner (2♀♀ and 1♂ on slides, 4♀♀ and 1♂ on points); Mt. Rainier National Park, Van Trump Park, 1500-1800m, 29.VII.1985, L. Masner, subalpine meadows and forest (20♀♀ and 6♂♂ on points, CNCI, USNM, BMNH).
Diagnosis. Female. Differs from all other North American *Anaphes* by the following combination of attributes: F3, 5 and 6 with 2 sensory ridges, F4 narrower, with 1 sensory ridge, remaining flagellomeres without sensory ridges; F2 at least 4.7 times as long as its apical width and at least 3.0 times as long as F1. Fore wing relatively large (long and wide) compared to body.

Description. Female. Colour. Dark brown; scape, pedicel and legs, especially fore legs, brown to light brown, sometimes yellowish. Fore wing with brown infuscation behind venation and narrowly along posterior margin almost to apex. Both wings with slight brown suffusion.

Body length. $\bar{x}$=696 (558-818, n=12).

Head. Head width 252 (224-281, n=8); occipital suture represented by short line almost parallel to posterior orbit, extending ventrally at least to level midway between dorsal and ventral margins of foramen magnum. Length of antennal articles (n=10): radicle+scape 152 (134-167); pedicel 63 (54-79); F1-F6 33 (30-36), 106 (90-128), 102 (96-159), 94 (84-109), 89 (80-102), 82 (75-92); club 162 (136-180). F3, F5 and F6 each with 2 sensory ridges, F4 with 1 sensory ridge (Fig. 38).

Mesosoma. Mesoscutum width 212 (167-235, n=6).

Wings. Fore wing length 1104 (973-1234, n=10), width 268 (209-335), posterior margin straight or very slightly concave (Fig. 22); length of marginal space 160 (136-211); FWW/FWL about 4.2 (3.68-4.69); LMC about 168 (136-192), about 0.6 times wing width. Hind wing length 992 (881-1100), width 51 (41-64); LMC/HWW about 3.2.

Metasoma. Ovipositor length 329 (273-387, n=10), about 0.9 times hind tibial length, extending anteriorly at most to halfway between base and apex of middle coxa.

Male. Similar to female. Length of antennal articles (excluding F1 which is minute) (n=2): radicle+scape 140 (129-152); pedicel 53 (44-63); F2-F11 140 (120-159), 141 (130-151), 141 (127-155), 139 (127-150), 134 (121-146), 127 (112-142), 130 (≈111-149), 134 (120-147), 132 (124-140) 133 (126-141).

Distribution. Northwestern USA and boreal Canada. Specimens examined were collected in July and August. The holotype and allotype were reared from their respective hosts in March, presumably under laboratory conditions.

Hosts and Biology. ex. *Lioon simplicipes* (Mannerheim) and *Lioligus nitidus* (Motschulsky) (Byrrhidae) in moss.

Comments. This species was mentioned by Schauff (1984a: 48) as "an undetermined species, probably new" in his discussion of *Anaphes* hosts. It is the largest North American species of *Anaphes*.

Anaphes alaskae Annecke and Doutt

Anaphes alaskae Annecke and Doutt, 1961: 47; Burks, 1979: 1028.

Type material. Holotype ♀ (CISC) [examined]. On slide under 4 cover slips, labelled: 1."Berlese funnel? Holotype Point Barrow, Alaska July 17, 1952 P.D. Hurd". 2."*Anaphes alaskae* n. sp. HOLOTYPE Det. D.P. Annecke and R.L. Doutt".

Diagnosis. Female. Differs from all other North American *Anaphes* by the following combination of attributes: blunt and widely rounded apex of club, F4 with 1 (occasionally 0) sensory ridge, F4 at most 2.7 times as long as wide, tarsomere 1 of hind leg about 1.5x as long as tarsomere 2.

Description. The species was well described and illustrated by Annecke and Doutt (1961) so measurements and descriptive notes only are given here based on the few specimens examined.

Female. Colour. Body dark brown; legs, scape and pedicel brown. Fore wing narrowly brown along posterior margin.

Body length. $\bar{x}$=852 (742-973, n=6).

Head. Head width 296 (289-303, n=2); occipital suture represented by short line almost parallel to posterior orbit, extending ventrally to level of dorsal margin of foramen magnum. Length of antennal articles (n=2): radicle+scape 164 (163-165); pedicel 66 (62-69) F1-F6 34 (32-36), 61 (60-63), 63 (60-66), 57 (56-58), 50 (no variation), 53 (53-54); club 164 (161-166). F3-5 each with 1 sensory ridge, F6 with 2 sensory ridges. Club apex bluntly rounded.

Mesosoma. Mesoscutum width 237 (n=1).

Wings. Fore wing length 966 (951-982, n=2), width 182 (171-194), posterior margin straight; length of marginal space 164 (145-183); FWW/FWL about 5.3 (5.13-5.54, n=2); LMC 140 (133-147), about 0.77 times wing width. Hind wing length 915 (886-944), width 38 (3740); LMC 151 (136-166); LMC/HWW about 4.0.

Metasoma. Ovipositor length 343 (n=1), about 1.0 times hind tibial length, extending anteriorly at most to apex of hind trochanter.

Male. See Annecke and Doutt (1961).

Distribution. North America, north of the Arctic circle. The specimens examined were collected in June and July.

Material examined. 8♀♀ (2 on slides).

CANADA. **Northwest Territories.** Victoria Island, 71°17'N, 114°W, 8-10 and 23-28.VII.1975, G.and M. Wood (4♀♀, CNCI). **Yukon.** Dempster Highway km 155 28.VI-2.VII and up to 16.VII.1982 (3♀♀, CNCI); Herchel Island, 7-16.VII.1971, W.R.M. Mason (1♀, CNCI).

Hosts and Biology. Unknown. The specimens examined were collected in pan traps on a south-facing tundra slope (Victoria Island) and at 4000' (Dempster Highway).

Comments. The specimens identified here as *A. alaskae* have the antennal proportions almost the same as described by Annecke and Doutt (1961) but are smaller than the holotype. I have seen many more female specimens from the localities listed above which have relatively longer flagellomeres. Possibly, these specimens should also be included in *A. alaskae* but until something is known about the hosts of this species and reared series can be obtained to assess variation, I prefer to restrict the species concept to those specimens most resembling the original description.

Anaphes nigrellus Girault
(Figs. 23, 39)

Anaphes nigrellus Girault 1911e: 282; Girault 1911b: 135; Girault 1911c: 188; Girault 1912a: 89; Frison 1927: 227; Girault 1929: 14; Burks 1979: 1029.

Mymar nigrellus; Soyka 1949: 332; Peck 1951: 416; Pec, 1963: 39.

Anaphes behmani Puttler *et al.* 1973: 1304 (misidentification).

Type material. HOLOTYPE ♀ (INHS). On slide labelled: 1."Type ♀ *Anaphes nigrellus* Girault". 2."Property of the Illinois Natural History Survey". 3."Urbana Ill., June 26 '09. J.D. Hood. *Anaphes nigrellus* Girault Flew into dish of xylol on table at Laboratory 44,228 Type S.1520". The holotype is in good condition, mounted laterally with head and propleura broken off and positioned face down. Girault (1911e) described this species from 1 specimen only.

Girault (1911e) examined 2♀♀ and 1♂ in addition to the holotype, none of which can be considered as type material although Girault labelled one female as "cotype" no. 13,808. Neither the "cotype" specimen in the USNM or the female collected at Urbana on October 19, 1910 (?INHS) could be found. The ♂ specimen labelled "Univ. Chicago. Allen. 554", which Girault claimed was undoubtedly one of *A. nigrellus*, was examined (slide mount, USNM).

Diagnosis. Female. Most similar to *A. hercules*. Both species have at least 1 sensory ridge on F2 of at least one antenna.

Description. Female. Colour (from faded specimens). Brown; legs, scape and pedicel laterally yellowish. Fore wing with faint brown infuscation along anterior margin and narrowly along posterior margin.

Body length. $\bar{x}$=539 (486-602, n=9).

Head. Head width 247 (229-251, n=5); occipital suture represented by line extending ventrally to level of ventral margin of foramen magnum. Length of antennal articles (n=7, except scape n=3): radicle+scape 136 (116-149); pedicel 52 (49-58); F1-F6 24 (23-26), 58 (42-62), 71 (65-75), 70 (63-73), 69 (64-74), 67 (64-72); club 122 (110-134). F3-6 each with 2 sensory ridges, F2 with 1 sensory ridge, although one specimen had 2 sensory ridges on one antenna (Fig. 39).

Mesosoma. Mesoscutum width 182 (171-200, n=4).

Wings. Fore wing length 730 (669-781, n=7), width 127 (105-141), posterior margin slightly concave (Fig. 23); length of marginal space 95 (88-105); FWW/FWL about 5.8 (5.26-6.37); LMC 139 (124-155), about 1.09 times wing width. Hind wing length 695 (640-738), width 30 (25-31); LMC/HWW about 3.93.

Metasoma. Ovipositor length 241 (215-272, n=7), about 0.9 times hind tibial length, extending anteriorly at most to apex of hind coxa.

Male. Similar to female. Length of antennal articles (excluding F1 which is minute) (n=1): radicle+scape 96; pedicel 28, F2-F11 68, 73, 73, 74, 67, 71, 72, 74, 69, 73.

Distribution. North America. Specimens were collected in May, July, and August.

Material examined. 13♀♀ and 3♂♂ (10 on slides).

CANADA. **Ontario.** London, Fanshawe Experimental Farm, 4-25.VIII.1982, A. Tomlin (6♀♀, CNCI), same locality but 3-12.VII.1982 (1♀, CNCI).

USA. **Missouri.** *Carrollton Co.*: Carrollton 18.V.1969, B. Puttler (CNCI, UMRM).

Hosts and Biology. Curculionidae. *Hypera compta* (Say), *H. eximia* (LeConte), *H. paludicola* Warner, *H. postica* (Gyllenhal) (Puttler *et al.* 1973). The specimens from London were collected from pan traps in an onion field. Mr. B. Puttler (pers. comm.) believes that *A. nigrellus* exhibits habitat preference with a behavioural response to moist environments which are the primary habitat of its hosts, *Hypera compta*, *H. paludicola* and *H. eximia*, and host plants. *H. postica* only served as a laboratory host. The host eggs are laid inside leaf tissue or stems. In contrast, *A. flavipes*, which I cannot separate reliably from *A. nigrellus*, parasitizes host eggs (*Oulema melanopus* and relatives) which are exposed on the plant surface.

Comments. I consider that the species reared from *Hypera* spp. by Puttler *et al.* (1973) and identified as *A. behmani* belong to *A. nigrellus*.

Because of the difficulty of reliably associating males and females of *Anaphes* and the small differences that separate the species I am not certain that the male identified by Girault as *A. nigrellus* really belongs to that species. Only the discovery of a host and subsequent association of the sexes by rearing can give an unequivocally correct association of sexes. Nevertheless, for the present, the male discussed by Girault is considered as being that of *A. nigrellus*.

A. nigrellus has no features that make it readily distinguishable. Many specimens were examined that may belong to *A. nigrellus* but they differ slightly in antennal proportions. Whether this represents intraspecific variation or specific differences cannot be resolved at present. Possibly, *A. behmani* should be synonymized under *A. nigrellus* but if so then both, in turn, should also be synonymized under *A. flavipes* because the differences among all three species are about the same. The definitions of the three species involve the relative lengths of F2 and F3 and the presence or absence of sensory ridges. One point-mounted specimen (from Carrollton) considered

here as *A. nigrellus* has one antenna with F3 1.6 times longer than F2 and about the same width whereas the other antenna has F3 only 1.17 times longer than F2 but distinctly wider. The sensory ridges on this specimens could not be seen but it is likely that one antenna had at least one sensory ridge on F2 whereas the other did not. In the absence of sufficient biological data this kind of variation would suggest that *A. nigrellus* and *A. behmani* (and probably other species such as *A. flavipes*) should be synonymized. I have not done this because of the biological observations by B. Puttler on habitat preference and location of host eggs that appear to support the distinctness of these two species.

Anaphes hercules Girault
(Figs. 26, 40)

Anaphes hercules Girault 1911e: 285; Girault 1911d: 364; Girault 1912a: 89: Frison 1927: 227; Girault 1929: 14; Burks 1979: 1029.
Mymar hercules; Soyka 1949: 331; Peck 1951: 416; Peck 1963: 39.
Type material. HOLOTYPE ♀ (INHS). On slide labelled 1."Mymarids *Anaphes hercules* [one illegible word follows] Girault ♀ Urbana, Illinois Type: June 8, 1910. 44242. Girault S1504". 2."Property of the Illinois Natural History Survey". 3."*Polynema consobrinus* Girault ♀ paratype [in pencil]". 4."Type *Anaphes* ♀ *hercules* Girault". The holotype is in fairly good condition, mounted dorsal side up with head detached and face up. The right flagellum beyond the pedicel is missing and the left antenna is poorly oriented and partly collapsed so that the basal articles cannot be measured accurately (Fig. 40).
Diagnosis. Female. This species is known only from the holotype whose measurements are given in Appendix I. It is tentatively separated from related species by the attributes given in the key. The fore wing (Fig. 26) is slightly larger than in related species but is otherwise similar to them in shape and setation.
Distribution. North America, Illinois.
Material examined. Holotype.
Hosts and Biology. Unknown.
Comments. The reference by Hartung (1919), quoted in Thompson (1958: 568) is probably incorrect but because I have not seen any voucher material I cannot determine the species involved. The reference to *Anaphes* nr. *hercules* (Flock *et al.* 1962: 278) is, in fact, *Anaphes iole* Girault (Huber and Rajakulendran 1988). Viereck (1923: 235) recorded a species nr. *hercules* from the Pribilof Islands. I have not seen specimens of this so cannot identify it. Judging from its large size and provenance, the species may be *A. byrrhidiphagus*.

Anaphes flavipes (Förster)
(Figs. 24, 41)

Gonatocerus flavipes Förster 1841: 45; Walker 1846: 53; Kirchner 1867: 201.
Anaphes flavipes; Förster 1847: 212; Loew 1847: 341; Kirchner 1867: 202: Dalla Torre 1898: 423; Schmiedeknecht 1909: 499; Debauche 1948: 160; Soyka 1949: 310; Anderson and Paschke 1968: 1; Anderson and Paschke 1969: 1316; Anderson and Paschke 1970a: 821; Anderson and Paschke 1970b: 107: Moorehead and Maltby 1970a: 675; Moorehead and Maltby 1970b: 1; Barton and Stehr 1970: 128; Bakkendorf 1970: 154; Maltby *et al.* 1971: 693; Morris and

Moorehead 1971: 41; Bjegovic 1971: 20; Dysart 1971: 445: Burger and Holmes 1972: 1185; Miczulski 1973: 98; Puttler *et al.* 1973: 1304; Maltby *et al.* 1973: 298; Stehr *et al.* 1973: 453; USDA 1972, 1974: 2; Hellén 1974: 25; Haynes *et al.* 1974: 167; Diadechko and Ruban 1974: 27; Aeschlimann 1975: 407; Favinger 1976: 227; Greathead 1976: 128; Bouček 1977: 122; Pavlov 1977: 151; Clausen 1978: 253; Trjapitzin 1978: 530; Burks 1979: 1029; Burger 1980: 39; Haynes and Gage 1981: 269; Pavlov 1981: 116; Hinton 1981: 238; Collins and Grafius 1983: 2; Lampert *et al.* 1983: 973; Staines 1984: 435; Lampert and Haynes 1985: 74; Huber 1986: 197; Davidson and Lyon 1987: 178; Hua 1987: 41; Trjapitzin 1987: 964; Donev 1987: 69; Ellis *et al.* 1989: 43; Glogowski 1989: 240.

Anaphes lemae Bakkendorf 1970: 153; Miczulski 1973: 98; Bouček 1977: 122; Trjapitzin 1978: 530; Collins and Grafius 1983: 2; Trjapitzin 1987: 964. **Syn. n.** (see comments below).

Patasson valkenburgica; Bakkendorf 1964: 3. (misidentification; corrected in Bakkendorf 1970: 153).

Anaphes sp.; Stehr 1969: 1.

Type material. ***Gonatocerus flavipes***. ?SYNTYPES (NHMW) [not examined]. The types were collected in Aachen, West Germany. Debauche (1948) believed that the species was described from a single specimen but did not mention that he had examined it. Soyka (1949) may have been the last and perhaps only person to have examined Förster's types of *Anaphes*, including *A. flavipes*, since they were described. He stated that the types were in too poor a condition to allow the species to be recognized. I searched for the Förster types in Vienna but, except for those of *A. pratensis*, could not find any of them.

Anaphes lemae. HOLOTYPE ♀ (ZMUC, Copenhagen) [examined]. On slide labelled: 1."*Anaphes lemae* Bkdf. ♀ Holotype. Lubin (city area) Poland Ex *Oulema* sp. leg. Miczulski prep. Bakkendorf". The holotype is in good condition, mounted laterally, uncleared, with club of left antenna collapsed. PARATYPES. 1♀ and 1♂ (USNM), with same data as holotype, in good condition. They are the same as *A. flavipes* in my opinion. Although the synonymy of *A. lemae* with *A. flavipes* was assumed by several workers (Dysart 1971; Miczulski 1973) it was never formalized so I synonymize them formally here.

Diagnosis. Female. This species cannot be adequately distinguished from *A. behmani* on morphological grounds. Both have a relatively short F2 without sensory ridges. Both are distinguished from *A. nigrellus* and *A. hercules* by F2 without sensory ridges (the latter each have 1 or 2).

Description. The description is based on reared specimens introduced from Europe into quarantine at the Biological Control Laboratory, USDA, Niles, Michigan. Colour is described from freshly collected (reared) and critical point dried specimens from North Carolina. **Female.** Colour. Dark brown, scape and pedicel laterally, and legs beyond coxae pale brown; tarsi slightly darker than rest of legs. Fore wing with faint brown infuscation behind venation.

Body length. $\bar{x}$=568 (409-657, n=10).

Head. Head width 242 (217-274, n=8); occipital suture represented by line extending ventrally to level of ventral margin of foramen magnum. Length of antennal articles (n=11): radicle+scape 121 (113-132); pedicel 49 (44-52); F1-F6 25 (21-30), 54 (36-66), 69 (57-76), 69 (52-78), 71 (60-78), 69 (53-76); club 125 (114-135). F3-6 subequal in width, each with 2 sensory ridges (Fig. 41).

Mesosoma. Mesoscutum width 177 (140-206, n=8).

Wings. Fore wing length 670 (559-747, n=11), width 90 (73-112), posterior margin slightly concave (Fig. 24); length of marginal space 108 (88-123); FWW/FWL 7.34 (6.65-7.89); LMC 137

(124-151), about 1.5 times wing width. Hind wing length 658 (568-715), width 25 (19-29); LMC 137 (124-151); LMC/HWW about 4.6.

Metasoma. Ovipositor length 248 (198-283, n=10), about 1.0 times hind tibial length, extending anteriorly at most to apex of mid tibia.

Male. Similar to female. Length of antennal articles (excluding F1 which is minute) (n=6): radicle+scape 100 (88-105); pedicel 43 (38-44); F2-F11 70 (59-76), 72 (62-78), 71 (63-75), 71 (64-78), 71 (64-76), 70 (64-75), 71 (63-76), 71 (64-70), 69 (62-72), 72 (68-75).

Distribution. Europe (see Dysart 1971, for distribution map and localities) and eastern North America. Field collected specimens from North America were collected mostly in June and July.

Material examined. 293♀♀ and 75♂♂ (302 on slides).

CANADA. **Ontario**. Delhi, 25.V.1988, C. Ellis (1♀, DEBU).

POLAND. no locality, 17.XII.1969, G.E. Moorehead (23♀♀ and 11♂♂, USNM).

RUMANIA. no locality, VI.1968, G.E. Moorehead (2♀♀ and 2♂♂, USNM).

AUSTRIA. no locality, VI.1968, G.E. Moorehead (4♀♀ and 2♂♂, USNM).

YUGOSLAVIA. no locality, 18.VIII.1967, T.L. Burger (12♀♀ and 3♂♂, USNM); no locality or date, P. Bjegovic (5♀♀, USNM).

ITALY. Rome, 17.V.1965, J.J. Drea (1♀, USNM).

FRANCE. Nanterre, 7.VII.1964, G.W. Angalet, and 28.V.1965, R.I. Sailer (2♀♀, USNM); Tours, 27.VI.1968, L. Dureseau (10♀♀ and 5♂♂, USNM) and 16.VI.1970 (4♀♀, USNM).

USA. **Michigan.** *Allegan Co.*: 29.IV.1968, T.L. Burger (3♀♀, USNM); *Berrien Co.*: Bertrand township, 3.VII.1975, P.R. DeWitt (2♀♀ and 2♂♂, USNM); Niles, 6.VII.1967, 2.X.1967, 10.VII.1969, 12.VI.1970, H. Maltby, T.L. Burger, F. Wilkinson, G.E. Moorehead (41♀♀ and 14♂♂, USNM), 1975 (5♀♀, USNM), 1977 (11♀♀ and 7♂♂, CNC); *Branch Co.*: 1975 (23♀♀, USNM); *St. Clair Co.*: 1975 (15♀♀, USNM). **Maryland.** *Baltimore Co.*: 1975 (18♀♀, USNM); *Washington Co.*: 25.VII.1975, P.R. DeWitt (2♀♀ and 2♂♂, USNM), 1975 (14♀♀, USNM). **New York.** *Ontario Co.* 1975 (13♀♀, USNM). **North Carolina**. *Granville Co.* 17.v.1991, D.I. Puttler (4♀♀ and 1♂, CNCI); *Rowan Co.* 16.v.1991 (15♀♀ and 3♂♂, CNCI). **Pennsylvania**. *Armstrong Co.*: 25.VII.1975, P.R. DeWitt (3♀♀ and 1♂, USNM), 1975 (17♀♀, USNM). **West Virginia**. *Mason Co.*, 1975 (19♀♀, USNM).

Hosts and Biology. Chrysomelidae: *Oulema melanopus* (L.) [cereal leaf beetle], *O. gallaeciana* (Heydon) (from Tours), *Oulema collaris* (Say), *Lema trilineata* Oliver (Anderson and Paschke 1969), *L. trilineata trivittata* (Say) (Maltby *et al.* 1971), *L. lichenis* Voet. (Bakkendorf 1970; Pavlov 1981), and *L. cyanella* (L.) (Miczulski 1973).

A. flavipes was imported into North America in 1966 for biological control of *O. melanopus* and the first evidence of establishment was obtained in 1968 (Maltby *et al.* 1971). North American material originated from specimens collected in several European countries (Dysart 1971; Miczulski 1973). The specimens examined by me from Poland, Austria, Rumania, Yugoslavia, Italy, Canada and USA were all reared from *O. melanopus*.

Comments. *Anaphes flavipes* belongs to a large complex of very similar species within the *fuscipennis* group, most of which were described by Debauche, Girault and Soyka. All of the species have 2 sensory ridges on F3-6 at least, and the fore wing similar in shape and coloration (posterior margin rimmed with brown). The three described native species that belong to this complex in North America, *A. behmani*, *A. hercules*, *A. nigrellus*, and those described from Europe have been differentiated on minor differences in proportions of the female flagellomeres, such as the length of F2 relative to F3, club length relative to F5 and F6, and pattern of microtrichia on the fore wing (Debauche 1948; Girault 1929). It appears that F2 and the club are the only flagellomeres that vary among the species, F1 and F3-6 being approximately the same in all of

them. There also appears to be considerable intraspecific variation in the length of F2 in at least one species, *A. nigrellus*, and this is correlated with the number of sensory ridges on F2 (0, or 1 - 2).

Hosts have been recorded for only two of the North American species - *A. nigrellus* and *A. behmani* (host possibly incorrect for the latter), and almost none of the species described by Debauche or Soyka. Most of the species, such as those of Soyka, were described from limited material and their specific status is doubtful. Much more material must been studied to assess variation and, most importantly, additional reliable host records obtained before these names can be applied meaningfully. Experimental rearing of a species from different hosts to determine if host-induced structural variation occurs, and cross breeding parasites from different hosts would be very desirable. If this is done it is likely that many more synonyms of *A. flavipes* will eventually be found among the nominal species proposed by Soyka, at least.

Because of its potential as a biological control agent there is a considerable literature, including at least one thesis (Barton 1968) referring to *A. flavipes*. The reference to *A. flavipes* in Graham (1982: 208) is accidental; it refers correctly to *A. auripes* Walker.

Anaphes behmani Girault
(Figs. 25, 42)

Anaphes behmani Girault 1929: 14; Burks 1979: 1029; Collins and Grafius 1983: 2;
Mymar behmani; Soyka 1949: 331; Peck 1951: 416: Peck 1963: 39.

Type material. LECTOTYPE ♀ (USNM), here designated. On slide labelled: 1."Emerged July 12 from larvae of *Dibolia borealis*" [in pencil]. 2." Type No. 20015 U.S.N.M.". 3."LECTOTYPE ♀ *Anaphes behmani* Girault des. Huber 1987". 4."*Anaphes behmani* Girault ♂ ♀ types. *behmani* Ithaca, N.Y.". The lectotype is in good condition under 1 coverslip with 2 other specimens. It is the specimen which is mounted ventral side up with head detached and face up. PARALECTOTYPES, here designated: 4♀♀ and 3♂♂. One somewhat shrivelled female and a headless male are under the same coverslip as the lectotype. Three females and 1 male are under 1 coverslip on a second slide with same data as lectotype except the date given is July 4 and the specimens are labelled as cotypes. The specimens on the second slide are all more or less broken and partly crushed.

Girault's (1929) key constitutes the only description of this species. He did not state how many specimens he had examined nor did he give any locality data. The information given here is taken from the slides examined. The species was incorrectly entered in the Type Book of the U.S. National Museum as a manuscript species.

Diagnosis. Female. *Anaphes behmani* is part of a species complex including *A. flavipes*, *A. nigrellus* and *A. hercules*. It differs from *A. hercules* and *A. nigrellus* by the absence of sensory ridges on F2 (present in the other two). I cannot distinguish it morphologically from *A. flavipes*.

Description. Female. Colour. (only the type slides are available so colour cannot be described).

Body length. (estimated from slide-mounted lectotype). About 440µ.

Head. Head width 216 (n=1); occipital suture represented by line extending ventrally to level of ventral margin of foramen magnum. Length of antennal articles (n=3): radicle+scape 93 (90-99); pedicel 43 (42-44); F1-F6 22 (21-22), 42 (42-43), 59 (54-66), 59 (56-66), 60 (55-64), 56 (53-61); club 107 (106-107). F3-F6 each with 2 sensory ridges (Fig. 42).

Mesosoma. Mesoscutum width 162 (n=1).

Wings. Fore wing length 604 (583-627, n=3), width 88 (73-100), posterior margin very slightly concave (Fig. 25); length of marginal space 358 (310-400); FWL/FWW 7.0 (6.3-8.3); LMC about 135 (122-143) about 1.5 times wing width. Hind wing length 579 (556-602), width 21 (20-24); LMC 96 (91-101); LMC/HWW about 4.6.

Metasoma. Ovipositor length 209 (202-214, n=3), about 1.1 times hind tibial length, extending anteriorly at most to base of middle coxa.

Male. Similar to female. Length of antennal articles (n=2): radicle+scape 78 (77-79); pedicel 40 (38-41), F2-F11 61 (60-63), 60 (57-63), 60 (56-63), 58 (54-61), 59 (58-59), 58 (57-59), 57 (57-58), 56, - , 61.

Distribution. North America.

Material examined. The type series only was seen.

Hosts and Biology. *Dibolia borealis* Chevrolat (Chrysomelidae). The lectotype slide indicates that the specimen emerged from a larva. This clearly is incorrect because mymarids are all idiobiont egg parasites. It is possible, therefore, that the host record itself is wrong and the mymarid was simply found in a cage in which larvae of *D. borealis* were being reared while the true host was something else. Further rearings of eggs of *D. borealis* are required to confirm the host record.

Comments. The host record of *A. behmani* from *Circulifer tenellus* (Flock *et al.* 1962) is incorrect. I examined slide-mounted voucher specimens (in CISC) and the species concerned is *A. iole*. The host for these specimens was most likely *Lygus* sp. and not *Circulifer*.

I examined specimens reared from *Hypera* by Puttler *et al.* (1973) and consider them to be *A. nigrellus* rather than *A. behmani*. Although the specimens I received from Mr. Puttler were faded and mostly broken; 3 of the 4 reasonably intact females that I slide-mounted had sensory ridges on F2 (as for *A. nigrellus*) and 1 had none on F2 (as for *A. behmani*). If this small sample indicates that the number of sensory ridges on F2 is more variable than presently interpreted then *A. nigrellus* and *A. behmani* could be synonymized on the basis of this feature. Further, if the two species are synonymized then they, in turn, should also be synonymized under *A. flavipes*. For the present, however, I think it best to keep the three species separate on the basis of different hosts.

Review of the described species of *Anaphes (Yungaburra).*

At present, there are only 7 valid names (6 valid species) that can be referred to *A. (Yungaburra)*, 3 in Australia and 4 in Argentina. At least 17 undescribed species are reported from New Zealand (Noyes and Valentine 1989), and there are also numerous undescribed species from Australia and southern South America. When these species have been described, the number of species in *A. (Yungaburra)* will more approximate that in *A. (Anaphes)*, especially when the large number of names proposed by W. Soyka is reduced through synonymy.

The following key is modified from the two keys found in Ogloblin (1962) and Huber and Prinsloo (1990), respectively, and the descriptions by Ogloblin (1962). Notes on the species described by Ogloblin (1962) are based on examination of most of the type specimens.

Key to described species of *A.* (*Yungaburra*). Females.

1 Club entire (southern South America) (Fig. 11) 2
- Club divided into 2 articles (Australia) (Fig. 12) 4

2(1) Fore wing relatively wide, FWL/FWW at most 3.1; F2-F4 each with 2 sensory ridges . . . . . *A. amplipennis* Ogloblin
- Fore wing narrower, FWL/FWW at least 3.8; F2-F4 each with 1 sensory ridge at most 3

3(2) FWL/FWW about 4.6 (Fig. 35); F2 with 1 sensory ridge . . . . . *A. nunezi* Ogloblin
- FWL/FWW 3.8-4.1 (Fig. 36); F2 without sensory ridges . . . . *A. pucarobius* Ogloblin

4(1) Sensory ridges on F4-F6 J-shaped (Fig. 12) . . . . . *A. nitens* Girault
- Sensory ridges on F4-F6 straight 5

5(4) F2 with 2 sensory ridges; length/width of F3 or F4 greater than 4.0 . . . . . *A. tasmaniae* Huber and Prinsloo
- F2 usually without sensory ridges, occasionally with 2 sensory ridges on one antenna; length/width of F3 or F4 less than 2.4 . . . . . *A. inexpectatus* Huber and Prinsloo

Anaphes (*Yungaburra*) *amplipennis* Ogloblin

Anaphes (*Austranaphes*) *amplipennis* Ogloblin 1962: 49; De Santis 1967: 108.
Type material. HOLOTYPE ♀ (MLPA) [not examined]. The types of *A. amplipennis* are apparently lost (see *A. pucarobius*, below). The species appears to be distinct based on the description and illustrations provided by Ogloblin (1962). His figure of the holotype antenna has 7 instead of 6 funicular articles. Presumably, article 4 was accidentally drawn twice. Each article except F1 has 2 sensory ridges.

Anaphes (*Yungaburra*) *nunezi* Ogloblin
(Fig. 35)

Anaphes (*Austranaphes*) *nunezi* Ogloblin 1962: 51; De Santis 1967: 109.
Type material. HOLOTYPE ♀ (MLPA). On slide labelled: 1."*Clinomymar* [crossed out in pencil] *Yungaburella* [in pencil] *nuñezi* ♀ A. Ogl. Puerto [crossed out in ink] Bahia Aguírre Tierra del Fuego. 14.ii.1949. Josué Nuñuz leg!". 2."HOLOTYPE *Anaphes* (*Austranaphes*) *nunezi* Ogloblin ♀". The holotype is in good condition, dorsal side up. Ogloblin (1962) described the species from two specimens which I examined.
Descriptive notes. Member of the *amplipennis* group. This species is distinct from the other species described by Ogloblin on the basis of its large size and distribution of sensory ridges on the flagellomeres. There are probably eight sensory ridges on the club, not seven as given by Ogloblin (1962).

Anaphes (*Yungaburra*) *pucarobius* Ogloblin
(Fig. 36)

Anaphes (*Austranaphes*) *pucarobius* Ogloblin 1962: 52; De Santis 1967: 109.
Anaphes (*Austranaphes*) *neuquenensis* Ogloblin 1962: 54; De Santis 1967: 109. **Syn. n.**
Type material. ***Anaphes pucarobius.*** HOLOTYPE ♀ (MLPA). On slide labelled: 1." 1 *Anaphes Austranaphes amplipennis* [crossed out in pencil] ♀ *pucarobius* [poorly written in dark pencil] A. Ogl. Pucará, Lago Lacar, Neuquen. 24 [in pencil] 23.ii.1953 V.K.O., A.A.O.". 2."Holotype *Anaphes* (*Austranaphes*) *pucarobius* Ogloblin ♀". The holotype is in good condition, dorsal side up. The date on the allotype was changed (in pencil) to 23.I.1953. Ogloblin (1962) described this species from one female and one male which I examined. The specimens and data correspond with the description of *A. pucarobius* and are definitely the types of that species. I added a label to each clarifying this because both were sent to me as *A. amplipennis*.
Anaphes neuquenensis. HOLOTYPE ♀ (MLPA). On broken slide labelled (entirely in pencil): 1."*persimilis* [crossed out] *neuquens* ♀ 1955.iii.18 "Holotypus" [followed by something illegible]". 2."3913". 3."♀ *persimilis* 32 [followed by something illegible]". 4."HOLOTYPE *Anaphes* (*Austranaphes*) *neuquenensis* Ogloblin ♀". The holotype is in good condition, dorsal side up. The specimen itself is undamaged though the slide it is on is broken and the pieces have been glued to another slide. Ogloblin (1962) described the species from one female and three males. I examined the holotype female and what must be one of the males. This male is labelled: 1."*persimilis* [in pencil] *Anaphes fimbriatus amplipennis* [crossed out] 30 A. Ogl. *fimbriatus* n.sp. Pucará, Lago Lacar. Terr. N. de Neuquen 24.II.1953 17-17 V.K. y A.A.O.". The date corresponds with one of the dates given in the description of *A. neuquenensis*. I measured the flagellomeres of this specimen and their length correspond well with the original description. Therefore I assume that this specimen is one of the males of *A. neuquenensis* even though there is no mention of this name on the slide. I added a label reading "*Anaphes* (*Austranaphes*) *neuquenensis* Ogloblin ♂" to clarify this. The antenna of this specimen is distinctly shorter than that of the male of *A. pucarobius* and the body is smaller. It may be that the specimen is not the male of *A. neuquenensis* at all but that of a new species, as Ogloblin indicated on the slide. The female corresponds exactly with that of *A. pucarobius* so I have synonymized the two species here. The slight differences given by Ogloblin to separate these two species are mostly due to the different orientation of the two holotypes on their respective slides.
Descriptive notes. Member of the *amplipennis* group. The number of sensory ridges on the female club of both types is difficult to count because the specimens are uncleared. Ogloblin (1962) enumerated seven but there are probably eight.

Anaphes (*Yungaburra*) *nitens* (Girault)
(Figs. 12, 18, 55, 59, 61, 63, 65, 67)

Anaphoidea nitens Girault 1928: 262.
Anaphoidea gonipteri Ferrière 1930: 38.

This species was redescribed by Huber and Prinsloo (1990). It is the type species of *Anaphes* (*Yungaburra*). I have since examined the two slides containing six specimens described by Dahms (1986). The five specimens (4♀♀, 1♂) on the same slide are paralectotypes and a label indicating this has been added to it. The specimens fall close to the upper limits of variation described by

Huber and Prinsloo (1990). In contrast, the specimen from Indooroopilly is smaller (FWL = 860µ, FWW = 273µ) than the lower limits given by Huber and Prinsloo (1990).

A. nitens is apparently widespread in Australia, specimens examined having been collected from Queensland (Indooroopilly), Tasmania (Hobart area) and West Australia (Lower Kalgan River). This species is the mymarid most cited in the literature, with over 100 references, due to its great success in the biocontrol of the eucalyptus snout beetle, *Gonipterus scutellatus* Gyllenhal.

Notes on types of the type species of several synonyms of *Anaphes*

I examined the type material of type species of 9 of the synonyms of *Anaphes*. Graham (1982) examined type material of *Panthus* and *Patasson* and stated that type specimen(s) of *A. punctum* (Shaw) seem to be lost. The types of *A.* (*Austanaphes*) *amplipennis* Ogloblin, are missing, as discussed above. The types of *Clinomymar peyerimhoffi* Kieffer have not yet been located but should be in the Museum National d'Histoire Naturelle, Paris. Some of the type specimens are discussed below with notes on their status and attributes that may help to make the species recognizable.

Anaphes pectoralis (Soyka)
(Figs. 28, 43)

Hofenederia pectoralis Soyka 1946b: 183; Soyka 1949: 338; Schauff 1984a: 48.
Hofenederia pinguicornis Soyka 1949: 392. **Syn. n.**

Type material. ***Hofenederia pectoralis.*** LECTOTYPE ♀ (NHMW), here designated. On slide labelled: 1."*Patasson* [in pencil] *Hofenederia* ♀ *pectoralis* Soyka det Soyka". 2."Co-Type". 3."66". 4."Hundsheim am Fenster-aus Heu 2 Juli 1944-lg Soyka Coll. Soyka In Canadab. 1945". 5."LECTOTYPE *Hofenederia pectoralis* Soyka ♀ des. Huber 1987". The lectotype is in good condition, mounted laterally with head detached and face up. PARALECTOTYPES, here designated, 1♀ (no. 1151, 6.VII.1944) and 1♂ (no. 67, VII.1940). Soyka (1946b) described this species from numerous females and males but did not designate a holotype. Soyka (1949) repeated his description and stated that there was one female type. In Vienna I found only two females, labelled as cotypes, and one male, labelled as a paratype. There is also one female with the same data as the holotype in Washington, D.C. (USNM paratype no. 59430). Because the original description did not specify a holotype, a lectotype is designated here.

Hofenederia pinguicornis. HOLOTYPE ♀ (NHMW) [not examined]. Soyka (1949) described this species from 1 "type" and 10 "cotypes". I consider the "type" to be a holotype designation and the remainder as paratypes. In Vienna I found two females and one male, all with the same label data (except for the sex and number) as follows: 1."*Hofenederia* ♀ [or ♂] *pinguicornis* Soyka". 2."Co-Type". 3."68"(♂), "69"(♀), or "1152"(♀). 4."Hundsheim am Fenster-aus Heu 2 Juli 1944-lg Soyka Coll. Soyka In Canadab. 1945". Two of the specimens also had "*Patasson*" written in pencil on the first label above "*Hofenederia*". The holotype, collected on 10.X.1941, is apparently lost. Although Soyka stated that males were unknown there is at least one in the paratype series.

Descriptive notes. Female. Member of the *crassicornis* group. In almost every respect the same as *A. iole* from North America except for the (incompletely) divided club and somewhat wider wings. Antenna (Fig. 43) with club divided by sulcus extending only about 3/4 distance around its circumference; F3-F6 evenly wide, each with 2 sensory ridges; scape with fine oblique striations on inner surface. Fore wing (Fig. 28) almost hyaline, hind margin without brown border except

at extreme apex; posterior row of microtrichia separated from hind margin by about one microtrichia length; FWL/FWW = 3.54-3.85 (n=2). Ovipositor extending forward to apex or base of middle coxae. Type measurements are given in Appendix II.

Comments. The type specimens of *A. pinguicornis* have a longer basal extension of the ovipositor and relatively shorter F2 than those of *A. pectoralis*. I consider these differences to represent infraspecific variation.

Anaphes hundsheimensis (Soyka)
(Figs. 29, 44)

Fulmekiella ***hundsheimensis*** Soyka 1946b: 184; Soyka 1949: 398; Soyka 1954: 63.

Type material. HOLOTYPE ♀ (NHMW). On slide labelled: 1."*Fulmekiella hundsheimensis* ♀ Soyka Geno-type". 2."Geno-Type". 3."1042". 4."Hundsheim am Fenster-aus Heu 6 Juli 1944-lg Soyka Coll. Soyka In Canadab. 1945". The holotype is in good condition, mounted laterally.

Descriptive notes. Female. Member of the ***crassicornis*** group. Antenna (Fig. 44) with club divided by sulcus extending only about 1/2 distance around its circumference; F4 with 1 sensory ridge, F3, F5 and F6 each with 2 sensory ridges; scape with fine, oblique striations on inner surface. Fore wing (Fig. 29) entirely margined with brown border, slightly lighter on basal half of posterior margin; FWL/FWW = 5.92. Ovipositor extending forward to mid point of fore coxa. Type measurements are given in Appendix II.

Anaphes superadditus (Soyka)
(Figs. 30, 45)

Mariella superaddita Soyka 1950: 123; Annecke and Doutt 1961: 23.

Type material. HOLOTYPE ♀ (NHMW). On slide labelled: 1."*Mariella* ♀ *superaddita* Soyka Type". 2."Type". 3."532". 4."Malkwitz b. Breslau Mai 1934 W. Soyka In Canadabalsam.". The holotype is in good condition, mounted laterally.

Descriptive notes. Female. Member of the *crassicornis* group. Somewhat similar to *A. maialis* Debauche which has two sensory ridges on F2. Antenna (Fig. 45) with club divided by a complete sulcus; F2 with 1 sensory ridge, F3-6 each with 2 sensory ridges; scape with oblique, rather faint striations. Fore wing (Fig. 30) entirely margined with brown except basal half of posterior margin; FWL/FWW=5.33. Ovipositor not produced beneath mesosoma; extending only to apex of hind coxa. Type measurements are given in Appendix II.

Anaphes stubaiensis (Soyka)
(Figs. 27, 46)

Fulmekiella stubaiensis Soyka 1949: 417; Annecke and Doutt 1961: 23.
Antoniella stubaiensis; Soyka 1950: 121.
Anaphoidea stubaiensis; Graham 1982: 212.

Type material. HOLOTYPE ♀ (NHMW). On slide labelled: 1."*Antoniella* ♀ *stubaiensis* Soyka Type". 2."Type". 3."1097". 4."Krössbach (Ranalter) am Fenster-aus Heu 15.Juli 1945 lg Soyka Coll. Soyka In Canadab. 1945". In good condition, mounted laterally with head detached and face

up, and one antenna under separate cover slip. In Vienna I found eight other specimens, each on a slide, which must all be considered as paratypes. All were collected at Krössbach but with the following numbers, dates and mostly incorrect type labels: 1098, 15.VII.1945, type (♂); 91, 11.VII.1945, cotype (♀); 92, 29.VII.1945, co-type (♂): 1099, 26.VI.1947 co-type (♀); 1100 and 1101, VII.1947, paratypes (2♂♂); 1102, 29.VII.1945 (1♂); 1103, 7.VII.1945 (1♀).

Descriptive notes. Female. Member of the ***crassicornis*** group. Antenna (Fig. 46) with club completely divided, although the suture is less distinct on one side than the other; F4 without sensory ridges, F3, F5 and F6 each with 2 sensory ridges; scape coarsely, almost transversely striate-imbricate on inner surface. Fore wing (Fig. 27) hyaline on posterior margin basally and apically except for a short brown stretch subapically; FWL/FWW=4.28-4.72 (n=5). Ovipositor extending forward almost as far as posterior margin of prosternum. Type measurements are given in Appendix II.

Comments. This species is almost identical to *A. collinus* Walker, as redescribed by Graham (1982). I have not synonymized *A. stubaiensis* with *A. collinus* because I have not seen the holotype of *A. collinus*. The species is also remarkably similar to *A. pallipes* (Ashmead). The wings of the holotype of *A. pallipes* are difficult to compare with other specimens because of their poor orientation. A specimen of *A. pallipes* from Connecticut, reared supposedly from *Ragoletis pomonella* (Walsh), has slightly wider wings than *A. stubaiensis* but is otherwise the same. Soyka (1949) originally described this species as *Fulmekiella* and later (Soyka 1950) made it the type species of *Antoniella*.

Anaphes wolfsthali (Soyka)
(Figs. 31, 47)

Stammeriella wolfsthali Soyka 1950: 120.

Type material. HOLOTYPE ♀ (NHMW). On slide labelled: 1."*Stammeriella* ♀ *wolfsthali* Soyka Genotype". 2."G.Type". 3."1142". 4."Wolfsthal, Rehfeld 27. Sept. 1941 lg Soyka In Canadab. 1941". The holotype is in moderately good condition, mounted dorsal side up with air bubbles in much of body; one fore wing, both antennae beyond pedicel, and right fore tarsus detached; club from one antenna missing.

Descriptive notes. Member of *crassicornis* group. Antenna (Fig. 47) with club barely divided by a trace of an incomplete sulcus extending only about half way around circumference; F4 with 1 sensory ridge, F5 and F6 each with 2 sensory ridges; scape with faint, oblique striations. Fore wing (Fig. 31) with marginal space extending almost entire wing length; posterior margin hyaline on apical one third; posterior row of microtrichia separated from hind margin by about 1 microtrichia length; FWL/FWW=4.87. Ovipositor extending forward to mouth parts (when head vertical). Type measurements are given in Appendix II.

Comments. This species exemplifies the problems of assigning unequivocally some species to a particular species group. Although the funicle resembles that of *A. fuscipennis* (in the *fuscipennis* group) I prefer to place *A. wolfthali* in the *crassicornis* group on the basis of the slightly and faintly divided club and the extremely long basal extension of the ovipositor.

Anaphes fabarius (Rondani)
(Figs. 34, 50)

Flabrinus fabarius Rondani 1877: 180; Bouček 1974: 248.

Type material. LECTOTYPE ♀ (MZUF), designated by Bouček (1974). On card point labelled: 1."LECTOTYPE" [small round white label with violet border]. 2."*Mimar fabarius*"[specific epithet not clearly legible]. 3."Lectotypus ♀ of *Flabrinus fabarius* Rondani 1877. = *Anaphes fabarius* (Rnd.) Bouček det. 1972." 4."60.". The lectotype is in reasonable condition, glued on its right side with wings, except for the basal half of the left hind wing, detached and glued next to the body. The left antenna is detached beyond the scape. The right antenna is detached beyond the radicle, and the scape, pedicel, F1, and F6 are missing; the flagellum is also broken between F4 and F5. Remaining parts of both antennae are glued next to the body.

Comments. Bouček (1974) correctly placed this species in *Anaphes*. I unglued the specimen to prepare one pair of wings and one antenna for illustration and to examine the length of the ovipositor which was largely hidden in glue. The specimen belongs to the *crassicornis* group on the basis of the almost completely divided club and the very long ovipositor extending to the base of the fore coxae.

Redescription. Colour. Uniformly very dark brown. Mouthparts and legs amber except for apical tarsomere of each leg, basal half of fore and middle femur, and hind femur which are brown. Scape and pedicel amber coloured laterally and ventrally. Basal half of ovipositor (under mesosoma) pale yellow. Fore and hind wings with faint uniform brown suffusion, both with anterior and posterior margins narrowly brown.

Total body length. 891µm. Club divided by a rather faint suture encircling only 3/4 of the club's circumference (Fig. 50). Inner surface of scape apparently smooth. Ovipositor extending forward almost to base of fore coxae. Type measurements given in Appendix II.

Anaphes intermedius (Soyka)
(Figs. 32, 48)

Ferrierella intermedia Soyka 1949: 344.

Type material. HOLOTYPE ♀ (NHMW). On slide labelled: 1."*Ferrierella* ♀ *intermedia* Soyka". 2."Type". 3."874". 4."Jettchen Hof b. Malchin Mecklenburg am Fenster Aug. 1936 lg Stammer In Canadab. 1941". The holotype is in good condition, mounted laterally. Soyka (1949) stated that there was one female and that males were unknown. In his collection there are three specimens (in addition to the holotype) which cannot be considered as part of the original type series. They are all from Hundsheim, as follows: no. 59 and no. 60, 26.VII.1943, paratype (1♀ and 1♂); 2.X.1941, type (1♂). The first two were collected "am fenster" and the latter was collected "am fenster Luzerne Heu". The USNM has two females with the same data as the holotype but collected in 1935. All are in good condition.

Descriptive notes. Female. Member of the *fuscipennis* group. Scape apparently smooth but trace of oblique sculpture present. Hind margin of fore wing pale brown in apical half. Base of ovipositor extending to base of mid coxa. Type measurements are given in Appendix II.

Anaphes medius (Soyka)
(Figs. 33, 49)

Anaphes medius Soyka 1946a: 40.
Synanaphes medius (Soyka) 1949: 334; Annecke and Doutt 1961: 20.
Anaphes ranalteri Soyka 1946b: 181. **Syn. n.**
Synanaphes ranalteri (Soyka) 1949: 333; Annecke and Doutt 1961: 20.
Synanaphes lacensis Soyka 1949: 335. **Syn. n.**
Anaphes (*Anaphes*) *fuscipennis sensu* Debauche 1948: 159.

Type material. ***Anaphes medius.*** HOLOTYPE ♀ (NHMW). On slide labelled: 1."*Synanaphes medius* ♀ Soyka". 2."Type". 3."1147". 4." Hundsheim am Fenster aus Heu 7 Juli 1943 lg Soyka Coll. Soyka In Canad. 1944". The holotype is in good condition, mounted laterally. Soyka (1946a) described this species from 1 female. Soyka (1949) redescribed the species and designated another female (no. 1146, 2.X.1941) and a male (no. 1145, 26.VII.1943) as "co-type" and "type", respectively. I examined both of these specimens. Neither specimen can be considered as type material (ICNZ rule 73(a)ii). There is one female from "Jettchenhof Malchin Mecklenburg" in the USNM. In the redescription, Soyka evidently had the wrong data for the cotype and quoted the date of collection of the holotype again.

Anaphes ranalteri. HOLOTYPE ♀ (NHMW). On slide labelled: 1." *Synanaphes ranalteri* ♀ Soyka Geno-Type". 2."Genotype". 3."1149". 4."Krössbach-Stubaital 12. Sept. 1946 Neustift-Tirol lg Soyka-Coll Soyk In Canad. 1946". The holotype is in good condition, mounted laterally. Soyka (1946b) stated that there was only one specimen, a female, and that the male was unknown. The original description has 1945, instead of 1946, as the collection date for this specimen. In his redescription, Soyka (1949) stated that there were 10 cotypes and males were unknown. I found only one female and three males besides the holotype in Vienna. Three of these specimens evidently formed part of Soyka's so-called co-typical series. They are labelled: no. 51, 5.IX.1946 (female cotype); no. 50, 27.VIII.1947 (male paratype); no.1148, 27.VIII.1947 (male genotype). The fourth slide, no. 1150, 27.VIII.1947 (male), was not labelled as a type. None of these specimens can be considered part of the type series (ICZN rule 73(a)ii). I did not locate the remaining six "co-types".

Anaphes lacensis. HOLOTYPE ♀ (NHMW). On slide labelled: 1."*Synanaphes* ♀ *lacensis* Soyka Type". 2."Type". 3."1144". 4."Jois, Neusiedlersee 7.Okt.1941 Soyka lg In Canadab. 1941". The holotype is in good condition, mounted laterally.

Descriptive notes. Female. Member of the *fuscipennis* group. Similar to *A. iole* Girault reared from *Lygus*. Antenna (Fig. 49) with club entire; F3-6 evenly wide, each with 2 sensory ridges; scape with fine, oblique striations on inner surface (cf. Soyka 1949). Fore wing (Fig. 33) almost hyaline, posterior margin narrowly rimmed with light brown at least on apical half of margin (as measured from apex of frenal fold); posterior row of microtrichia separated from posterior margin by about one half their own length; FWL/FWW = 5.0-5.4 (n=3). Ovipositor extended forward to base or apex of middle coxa. Type measurements are given in Appendix II.

Comments. I examined 18 slides (12♀♀ and 6♂♂) labelled as *A. fuscipennis* by Debauche and compared them with the types of *A. medius*. Nine of the females are definitely members of *A. medius*. All but one were collected in Belgium: Tervuren, 31.V.1945 and 23.VIII.1944; Héverlé, 1.X.1941;Campenhout, 5.IX.1941; Eegenhoven, 11.V.1942; and Forêt de Loverval, 10.VIII.1941. One was collected at Passo San Bernardino, 1500m, 20.VIII.1960 [Switzerland]. I am not certain about the placement of the three remaining females (Tervuren, 16.V.1945, no. 293; Revoz, Mirwart, M. Rémont, 19.VI.1945; and Eegenhoven, IX.1959). The males appear to represent a

mixture of species none of which seem to be members of *A. medius*. Graham (1982) suggested that *A. fuscipennis sensu* Debauche (1948) was possibly a synonym *A. ?brevis* Walker but because he could not find any type material of *A. brevis*, he was unable to confirm this.

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Checklist of *Anaphes* species.
(Gender: masculine)

The purpose of this list is to try and forestall further description of homonyms and to summarize the few, published, definite synonyms. All known names published before 1991 that have been referred to *Anaphes s.l.* are included. The genus or subgenus in which each species was originally placed is given in parentheses if this differs from *Anaphes* or its nominal subgenus. Species originally described as *Anaphes s.l.* that have been transferred to other genera are listed separately, together with the genus to which they have been transferred. In these cases, only the reference giving the transfer is cited, unless it is a new combination. Unavailable names are listed separately at the end. Doubtful synonyms proposed by previous authors e.g. Graham (1982) and Bakkendorf (1964) are excluded. The source of synonyms not proposed in the present paper is given in parentheses. There are 3 secondary homonyms in the list: *A. angustipennis* (Soyka) nec Debauche, *A. crassicornis* (Soyka) nec Walker, and *A. longicornis* (Soyka) nec Walker. It is pointless to propose replacement names for these until the European species are carefully revised. There are already enough names that need sorting out and adding more now would be counterproductive.

acutipennis (Soyka) 1949: 315 (*Mymar*)
acutiventris (Soyka) 1949: 419 (*Yungaburra*)
additus (Soyka) 1949: 354 (*Anaphoidea*)
aequipennatus (Soyka) 1953a: 37 (*Anaphoidea*)
aequus (Soyka) 1953a: 37 (*Anaphoidea*)
aestivus (Soyka) 1950: 121 (*Antoniella*)
alaskae Annecke and Doutt 1961: 47
albipes (Soyka) 1949: 355 (*Anaphoidea*)
amplipennis Ogloblin 1962: 49 (*Austranaphes*)
angustipennis Debauche 1948: 184 (*Patasson*)
angustipennis (Soyka) 1949: 339 (*Ferrierella*)
anomocerus, see *iole*; syn. of *iole* (Huber and Rajakulendran 1988)
antoniae (Soyka) 1955: 463 (*Mymar*)
apilosus (Soyka) 1949: 356 (*Anaphoidea*)
archettii Ghidini 1945: 39
arcuatus (Soyka) 1953a: 38 (*Anaphoidea*)
arenbergi Debauche 1948: 166
aries Debauche 1948: 1968
ater (Soyka) 1949: 400 (*Fulmekiella*)
aterrimus (Soyka) 1949: 399 (*Fulmekiella*)
atomarius (Brèthes) 1913: 100 (*Anaphoidea*)
auripes Walker 1846: 52
australia (Girault) 1920: 97 (*Anaphoidea*)
autumnalis Förster 1847: 212
avalae (Soyka) 1955: 464 (*Mymar*)
balteatus (Soyka) 1949: 401 (*Fulmekiella*)
basalis Förster 1861: 42
behmani Girault 1929: 14

bicolor (Soyka) 1953a: 38 (*Anaphoidea*)
brachygaster Debauche 1948: 176 (*Patasson*)
brevicornis (Soyka) 1949: 316 (*Mymar*)
brevior (Soyka) 1949: 357 (*Anaphoidea*)
brevis Walker 1846: 52
brevitarsis (Soyka) 1949: 340 (*Ferrierella*)
breviventris (Soyka) 1949: 341 (*Ferrierella*)
brunneus (Doutt) 1949: 159 (*Anaphoidea*)
byrrhidiphagus Huber sp.n.
calendrae (Gahan) 1927: 32 (*Anaphoidea*)
calvescens Debauche 1948: 180 (*Patasson*)
campestris (Soyka) 1949: 401 (*Fulmekiella*)
capitulatus (Soyka) 1949: 341 (*Ferrierella*); syn.n. of *fuscipennis*
chrysomelae (Bakkendorf) 1960: 372 (*Anaphoidea*)
ciliatus (Soyka) 1949: 317 (*Mymar*)
collinus Walker 1846: 52
communis (Soyka) 1949: 358 (*Anaphoidea*)
comosipennis Girault 1917: 17
compressus (Soyka) 1949: 360 (*Anaphoidea*)
confertus (Doutt) 1949: 155 (*Anaphoidea*)
congener Förster 1861: 42
conotracheli Girault 1905: 220
consimilis (Soyka) 1949: 402 (*Fulmekiella*)
crassicornis (Walker) 1846: 52 (*Panthus*)
crassicornis (Soyka) 1949: 318 (*Mymar*)
crassipennis Soyka 1946a: 41
crassipilis (Soyka) 1949: 360 (*Anaphoidea*)
crassus (Soyka) 1953a: 38 (*Anaphoidea*)
cultripennis Debauche 1948: 162
debilipennis (Soyka) 1949: 361 (*Anaphoidea*)
declinatus (Soyka) 1950: 121 (*Antoniella*)
depressus (Soyka) 1954: 63 (*Anaphoidea*); ?*lapsus* for *compressus*
dessarti (Mathot) 1969: 18 (*Patasson*)
devillei Debauche 1948: 177 (*Patasson*)
devius (Soyka) 1949: 403 (*Fulmekiella*)
diana (Girault) 1911a: 215 (*Anaphoidea*)
differens (Soyka) 1949: 363 (*Anaphoidea*)
dilatatus (Soyka) 1949, 342 (*Ferrierella*)
discolor (Soyka) 1949: 404 (*Fulmekiella*)
discolorsimilis (Soyka) 1950: 122 (*Antoniella*)
distinctus (Soyka) 1953a: 38 (*Anaphoidea*)
dorcas Debauche 1948: 179 (*Patasson*)
dubius (Soyka) 1949: 405 (*Fulmekiella*)
duplicatus (Soyka) 1953b: 53 (*Anaphoidea*)
dytiscidarum Rimskii-Korsakov 1920: 7
elegans (Soyka) 1955: 465 (*Mymar*)
elongatus (Soyka) 1949: 390 (*Hofenederia*)

ensipennis (Soyka) 1949: 320 (*Mymar*)
euryale Debauche 1948: 174 (*Patasson*)
exiguosimilis (Soyka) 1953b: 53 (*Anaphoidea*)
exiguus (Soyka) 1949: 363 (*Anaphoidea*)
fabarius (Rondani) 1877: 180 (*Flabrinus*)
falsus (Soyka) 1953b: 53 (*Anaphoidea*)
fennicus (Soyka) 1955: 465 (*Mymar*)
ferrierei (Soyka) 1946b: 180 (*Mymar*)
filicornis (Soyka) 1949: 343 (*Ferrierella*); syn.n. of *fuscipennis*
flavicornis (Soyka) 1949: 365 (*Anaphoidea*)
flavipennis (Soyka) 1954: 64 (*Anaphoidea*)
flavipes (Förster) 1841: 43 (*Gonatocerus*)
flavitarsis (Soyka) 1949: 364 (*Anaphoidea*)
flavus (Soyka) 1949: 321 (*Mymar*)
fortipennis (Soyka) 1953b: 53 (*Anaphoidea*)
fuscipennis Haliday 1833: 346
gabitzi (Soyka) 1953b: 54 (*Anaphoidea*)
galtoni Girault 1912b: 152 (*Anaphoidea*)
gauthieri Debauche 1948: 171
gerrisophagus (Doutt) 1949: 156 (*Anaphoidea*)
globosicornis (Soyka) 1949: 322 (*Mymar*)
globosus (Soyka) 1949: 366 (*Anaphoidea*)
gonipteri (Ferrière) 1930: 38 (*Anaphoidea*); syn. of *nitens* (Girault 1930)
gracilior (Soyka) 1949: 323 (*Mymar*)
gracillimus (Soyka) 1955: 466 (*Mymar*)
hercules Girault 1911e: 285
heterotomus (Mathot) 1969: 16 (*Patasson*)
hundsheimensis (Soyka) 1946b: 184 (*Fulmekiella*)
inexpectatus Huber and Prinsloo 1990: 340
intermedius (Soyka) 1949: 344 (*Ferrierella*)
iole Girault 1911e: 284
iole anomocerus Girault 1929: 13
kressbachi (Soyka) 1949: 367 (*Anaphoidea*)
lacensis (Soyka) 1949: 335 (*Synanaphes*); syn. n. of *medius*
lameerei Debauche 1948: 182 (*Patasson*); syn. of *dana* (Schauff 1984b)
laticornis (Soyka) 1949: 345 (*Ferrierella*)
latipennis Walker 1846: 52
latipterus Boţoc 1962: 111
latus (Soyka) 1949: 406 (*Fulmekiella*)
lemae Bakkendorf 1970: 153; syn. n. of *flavipes*
leonhardwitzi (Soyka) 1949: 324 (*Mymar*)
leptoceras Debauche 1948: 187 (*Patasson*)
linearis (Soyka) 1949: 407 (*Fulmekiella*)
lineipennis (Soyka) 1949: 368 (*Anaphoidea*)
linnaei (Girault) 1912b: 153 (*Anaphoidea*)
longiclavus (Doutt) 1949: 158 (*Anaphoidea*)
longicornis Walker 1846: 52

longicornis (Soyka) 1949: 407 (*Fulmekiella*)
longior (Soyka) 1949: 369 (*Anaphoidea*)
longipennis (Soyka) 1949: 370 (*Anaphoidea*)
longipilis (Soyka) 1954: 60 (*Anaphoidea*)
longispinosus (Soyka) 1955: 467 (*Mymar*)
lucidus (Soyka) 1949: 370 (*Anaphoidea*)
luna (Girault) 1914: 109 (*Anaphoidea*)
luteicornis (Soyka) 1955: 467 (*Mymar*)
maculatus (Soyka) 1949: 345 (*Ferrierella*); syn. n. of *fuscipennis*
maculicornis (Soyka) 1949: 390 (*Hofenederia*)
maialis Debauche 1948: 185 (*Patasson*)
malchinensis (Soyka) 1949: 392 (*Hofenederia*)
malkwitzi (Soyka) 1949: 408 (*Fulmekiella*)
medioacutus (Soyka) 1954: 60 (*Anaphoidea*)
medius Soyka 1946a: 40
minimus (Soyka) 1949: 371 (*Anaphoidea*)
minor (Soyka) 1949: 409 (*Fulmekiella*)
mirabilis (Soyka) 1955: 468 (*Mymar*)
nemorosus (Soyka) 1954: 60 (*Anaphoidea*)
neobrevior (Soyka) 1954: 60 (*Anaphoidea*)
neodistinctus (Soyka) 1954: 60 (*Anaphoidea*)
neoflavus (Soyka) 1949: 372 (*Anaphoidea*)
neopratensis (Soyka) 1946b: 182 (*Ferrierella*); syn. n. of *fuscipennis*
neoserenus (Soyka) 1955: 469 (*Mymar*)
neospecialis (Soyka) 1955: 469 (*Mymar*)
neuquenensis Ogloblin 1962: 54 (*Austranaphes*); syn. n. of *pucarobius*
neustadti (Soyka) 1949: 373 (*Anaphoidea*)
niger (Soyka) 1949: 411 (*Fulmekiella*)
nigerrimus (Soyka) 1949: 410 (*Fulmekiella*)
nigrellus Girault 1911e: 282
nigricornis (Soyka) 1949: 325 (*Mymar*)
nipponicus Kuwayama 1932: 93
nitens (Girault) 1928: 262 (*Anaphoidea*)
nunezi Ogloblin 1962: 51 (*Austanaphes*)
obscurus (Soyka) 1949: 374 (*Anaphoidea*)
obsoletus (Soyka) 1954: 61 (*Anaphoidea*)
ordinarius (Soyka) 1954: 61 (*Anaphoidea*)
ornatus (Soyka) 1949: 412 (*Fulmekiella*)
ovatus (Soyka) 1949: 413 (*Fulmekiella*)
ovijentatus (Crosby and Leonard) 1914a: 181 (*Anagrus*); syn. of *iole* (Girault 1929)
ovipositor Soyka 1946a: 41
pallidicornis (Soyka) 1949: 415 (*Fulmekiella*)
palliditarsis (Soyka) 1949: 375 (*Anaphoidea*)
pallidus (Soyka) 1949: 414 (*Fulmekiella*)
pallipes (Ashmead) 1887: 193 (*Alaptus*)
pannonicus (Soyka) 1946a: 42 (*Anaphoidea*)
parallelipennis (Soyka) 1949: 415 (*Fulmekiella*)

parciventris (Soyka) 1949: 376 (*Anaphoidea*)
parvus (Förster) 1841: 43 (*Gonatocerus*)
pectoralis (Soyka) 1946b: 183 (*Hofenederia*)
pellucens (Soyka) 1949: 377 (*Anaphoidea*)
perdubius Girault 1916: 6; syn. of *iole* (Girault 1929)
peyerimhoffi (Kieffer) 1913: 101 (*Clinomymar*)
piceicornis (Soyka) 1954: 61 (*Anaphoidea*)
pilicornis (Soyka) 1949: 326 (*Mymar*)
piliscapus (Soyka) 1949: 327 (*Mymar*)
pilosipennis (Soyka) 1949: 328 (*Mymar*)
pilosissimus (Soyka) 1954: 61 (*Anaphoidea*)
pinguicornis (Soyka) 1949: 392 (*Hofenederia*); syn.n. of *pectoralis*
pratensis Förster 1847: 211
pucarobius Ogloblin 1962: 52 (*Austanaphes*)
pulchripennis (Soyka) 1949: 348 (*Ferrierella*)
pullicrurus (Girault) 1910: 252 (*Anaphoidea*)
punctum (Shaw) 1798: 189 (*Ichneumon*)
quadraticornis (Soyka) 1949: 329 (*Mymar*)
ranalteri (Soyka) 1946b: 181 (*Synanaphes*); syn. n. of *medius*
rectipennis (Soyka) 1949: 378 (*Anaphoidea*)
reductus (Soyka) 1949: 379 (*Anaphoidea*)
regulus Walker 1846: 52
relictus (Soyka) 1949: 393 (*Hofenederia*)
rotundipennis (Soyka) 1949: 394 (*Hofenederia*)
rufus (Soyka) 1949: 416 (*Fulmekiella*)
saintpierrei Girault 1913: 117
schellwieniens Meunier 1901: 284
semiflavus (Soyka) 1949: 380 (*Anaphoidea*)
semimedius (Soyka) 1949: 381 (*Anaphoidea*)
serbicus (Soyka) 1949: 381 (*Anaphoidea*)
serenus (Soyka) 1955: 471 (*Mymar*)
sibbei (Soyka) 1954: 64 (*Anaphoidea*)
siegerfeldi (Soyka) 1955: 472 (*Mymar*)
silesicus (Soyka) 1946a: 42 (*Anaphoidea*)
similis (Soyka) 1949: 383 (*Anaphoidea*)
sinipennis Girault 1911e: 280
sordidatus (Girault) 1909: 169 (*Anaphoidea*)
speciosior (Soyka) 1954: 61 (*Anaphoidea*)
speciosus (Soyka) 1955: 472 (*Mymar*)
spinosus (Soyka) 1949: 330 (*Mymar*)
splendens Meunier 1901: 284
stammeri (Soyka) 1949: 349 (*Ferrierella*); syn. n. of *fuscipennis*
stratipennis (Soyka) 1954: 62 (*Anaphoidea*)
stubaiensis (Soyka) 1949: 417 (*Fulmekiella*)
stygius Debauche 1948: 165
sulphuripes (Soyka) 1949: 330 (*Mymar*)
superadditus (Soyka) 1950: 123 (*Mariella*)

swiedecki (Soyka) 1953b: 54 (*Anaphoidea*)
tarsalis Mathot 1969: 19
tasmaniae Huber and Prinsloo 1990: 338
tenuipennis (Soyka) 1949: 350 (*Ferrierella*)
tenuis (Soyka) 1949: 395 (*Hofenederia*)
thoracicus (Soyka) 1955: 473 (*Mymar*)
timidus (Soyka) 1950: 124 (*Mariella*)
valkenburgicus (Soyka) 1949: 385 (*Anaphoidea*)
variatus (Soyka) 1949: 384 (*Anaphoidea*)
varicolor (Soyka) 1949: 350 (*Ferrierella*)
vulgaris (Soyka) 1946a: 42 (*Anaphoidea*)
vulgarisimilis (Soyka) 1954: 62 (*Anaphoidea*)
weidenhofi (Soyka) 1954: 62 (*Anaphoidea*)
wertaneki (Soyka) 1955: 474 (*Mymar*)
wolfsthali (Soyka) 1950: 120 (*Stammeriella*)
wratislawensis (Soyka) 1954: 62 (*Anaphoidea*)

Species transferred from *Anaphes* to other genera.

bicolor (Dozier) (*Schizophragma*), Huber 1987: 834
cinctiventris (Girault) (*Erythmelus*), Girault 1929: 7
elongatus (Risbec) (*Anagrus*), Ghesquière 1951: 344
foersteri (Ratzeburg) 1848: 141 (*Anagrus*) **comb. n.**
gracilipes (Girault) (*Erythmelus*), Girault 1929: 7
gracilis (Howard) (*Erythmelus*), Girault 1929: 8
harveyi (Girault) (*Erythmelus*), Girault 1912b: 151 **comb. n.**
himalayana (Mani and Saraswat) (*Anagroidea*) Subba Rao and Hayat 1983: 131
kantii (Girault) (*Erythmelus*) Girault 1915: 179
laplacei (Girault) (*Erythmelus*) Girault 1915: 179
latipennis (Crawford) (*Schizophragma*) Ogloblin 1949: 350
mazzinini Girault (*Erythmelus*) Girault 1915: 179 (as *mazzinii*)
mellicornis (Ashmead) (*Amitus*-Scelionidae) Gahan 1927: 39
ovivorus Rondani (*Telenomus*-Scelionidae) Bouček 1974: 273
painei Girault (*Erythmelus*) Girault 1915: 179
picinus (Girault) (*Erythmelus*) Girault 1929: 8
spinozai (Girault) (*Erythmelus*) Girault 1915: 179
tingitiphagus (Soares) 1941: 265 (*Erythmelus*) **comb. n.**
wallacei (Girault) (*Erythmelus*) Girault 1915: 179

Unavailable name

nigroparvus (Soyka) 1954: 63 (*Fulmekiella*), **nom. nud.**

APPENDIX I. Measurements (in µm) of primary types of nominal species of *Anaphes s. s.* (*fuscipennis* group) for North America. Abbreviations used: Fem.=femur; FW=fore wing; HT=holotype; HW=hind wing; L=length; LT=lectotype; Macro. dist.=distance between macrochaetae of marginal vein; ovip.=ovipositor; PLT=paralectotype; Stig.=stigmal vein; Tib.=tibia; Troch.=trochanter; W=width. Many measurements could not be made because parts were missing or not clearly visible. Measurements of structures positioned obliquely or taken from air-dried specimens (*fuscipennis*) are not accurate, and are indicated by "≈". Types of *flavipes*, *iole*, and *sinipennis* are lost, presumably destroyed.

Nominal species	Type	Head W	Mesosoma		Ovip. L.	Ovip./hind tibia
			W	L		
1. *ovijentatus*	LT	-	-	345	401	1.62
2. *anomocerus*	LT	-	-	-	283	1.78
3. *perdubius*	LT	156	129	-	297	1.65
4. *alaskae*	HT	313	-	428	370	1.01
5. *behmani*	LT	194	168	213	215	1.09
6. *hercules*	HT	239	177	292	235	0.84
7. *nigrellus*	HT	253	-	275	214	0.88
8. *fuscipennis*	LT	257	228	297	436	≈1.50
9. *pratensis*	LT	-	-	379	513	1.42
10. *neopratensis*	HT	-	-	422	496	1.33
11. *maculatus*	HT	292	-	331	526	1.73
12. *filicornis*	HT	-	-	350	509	1.50
13. *capitulatus*	HT	-	-	263	377	1.60
14. *stammeri*	HT	-	-	335	464	1.47
15. *byrrhidiphagus*	HT	292	241	≈384	≈301	≈0.79
16. *lemae*	HT	-	-	≈253	-	-

APPENDIX I. - continued.

Nominal species	FW				Total ven. L	Macro. dist.	Stig. L	Marginal space L
	L	W	L/W	LMC				
1. *ovijentatus*	758	199	3.81	113	239	61	45	-
2. *anomocerus*	≈523	102	≈5.13	111	174	48	31	108
3. *perdubius*	617	132	4.67	127	205	60	29	107
4. *alaskae*	923	161	5.73	131	346	96	52	150
5. *behmani*	640	99	6.46	136	208	55	32	93
6. *hercules*	844	150	5.63	128	286	79	39	135
7. *nigrellus*	700	117	5.98	126	244	60	41	98
8. *fuscipennis*	≈802	≈168	4.76	≈238	≈238	-	-	≈99
9. *pratensis*	1034	215	4.81	193	336	88	43	148
10. *neopratensis*	1096	247	4.44	197	343	98	38	170
11. *maculatus*	904	212	4.26	167	276	69	34	160
12. *filicornis*	997	218	4.57	194	298	81	34	150
13. *capitulatus*	704	147	4.79	155	205	52	29	103
14. *stammeri*	888	189	4.70	159	281	73	39	140
15. *byrrhidiphagus*	1344	373	3.60	166	392	102	49	191
16. *lemae*	727	109	6.67	145	257	62	42	103

APPENDIX I. - continued.

Nominal species	HW			Ven. L
	L	W	LMC	
1. *ovijentatus*	715	37	109	238
2. *anomocerus*	466	21	81	155
3. *perdubius*	574	-	-	188
4. *alaskae*	901	40	130	330
5. *behmani*	≈560	21	100	185
6. *hercules*	821	37	120	275
7. *nigrellus*	632	25	99	200
8. *fuscipennis*	≈732	≈40	≈129	≈218
9. *pratensis*	987	52	171	337
10. *neopratensis*	1028	51	167	355
11. *maculatus*	854	44	137	269
12. *filicornis*	956	43	158	313
13. *capitulatus*	-	-	-	224
14. *stammeri*	848	-	-	283
15. *byrrhidiphagus*	1219	68	164	404
16. *lemae*	668	28	116	201

APPENDIX I. - continued.

Nominal species	Fore leg								
	Coxa	Troch.	Fem.	Tib.	Tarsus				
					Total	1	2	3	4
1. *ovijentatus*	70	49	169	155	170	45	45	42	33
2. *anomocerus*	-	-	108	110	117	29	32	30	25
3. *perdubius*	≈73	41	130	127	126	38	31	34	25
4. *alaskae*	151	75	238	218	≈200	67	44	38	≈44
5. *behmani*	73	47	128	125	135	43	33	32	28
6. *hercules*	110	58	189	184	177	52	47	42	38
7. *nigrellus*	92	44	164	156	160	51	40	35	32
8. *fuscipennis*	-	-	-	-	≈198	-	≈50	≈40	≈40
9. *pratensis*	≈129	-	≈249	≈222	-	74	47	-	-
10. *neopratensis*	-	-	≈244	≈237	250	94	59	53	47
11. *maculatus*	-	-	≈200	208	204	80	51	47	40
12. *filicornis*	-	-	-	216	241	90	57	50	43
13. *capitulatus*	91	46	165	156	170	62	40	37	33
14. *stammeri*	-	-	205	200	219	82	49	47	40
15. *byrrhidiphagus*	-	73	≈248	257	≈206	64	48	47	45
16. *lemae*	-	-	-	157	150	47	37	36	32

APPENDIX I. - continued.

Nominal species	Middle leg								
	Coxa	Troch.	Fem.	Tib.	Tarsus				
					Total	1	2	3	4
1. *ovijentatus*	61	46	150	206	-	35	47	44	35
2. *anomocerus*	-	-	-	-	-	-	-	-	-
3. *perdubius*	54	40	126	168	129	34	35	28	29
4. *alaskae*	-	75	237	296	209	72	50	45	49
5. *behmani*	57	45	127	173	129	32	33	35	29
6. *hercules*	-	62	193	279	173	45	48	46	36
7. *nigrellus*	≈56	45	159	≈216	152	38	43	38	33
8. *fuscipennis*	-	≈59	≈208	≈257	≈228	-	≈50	≈50	≈40
9. *pratensis*	-	≈66	≈227	322	272	111	62	55	45
10. *neopratensis*	-	-	251	344	261	113	58	53	43
11. *maculatus*	70	56	≈201	-	230	84	56	48	42
12. *filicornis*	87	-	227	313	254	104	61	50	43
13. *capitulatus*	68	-	164	215	173	61	41	37	33
14. *stammeri*	-	-	251	286	244	93	54	52	44
15. *byrrhidiphagus*	101	62	265	343	229	70	55	53	46
16. *lemae*	59	-	-	-	-	-	-	-	-

APPENDIX I. - continued.

Nominal species	Hind leg								
	Coxa	Troch.	Fem.	Tib.	Tarsus				
					Total	1	2	3	4
1. *ovijentatus*	104	62	188	250	167	36	48	47	35
2. *anomocerus*	-	-	-	159	116	18	33	31	25
3. *perdubius*	82	46	146	176	130	27	38	36	27
4. *alaskae*	-	98	306	369	259	98	62	56	48
5. *behmani*	83	53	142	193	130	32	34	34	31
6. *hercules*	120	70	≈188	287	212	55	62	54	41
7. *nigrellus*	90	60	196	244	176	44	51	44	36
8. *fuscipennis*	≈178	69	≈218	≈287	≈238	≈69	≈50	-	-
9. *pratensis*	157	86	291	329	279	115	62	56	49
10. *neopratensis*	166	76	298	371	259	109	59	53	44
11. *maculatus*	147	≈71	247	308	242	92	55	50	42
12. *filicornis*	-	-	≈269	339	264	107	62	53	44
13. *capitulatus*	109	64	195	230	180	64	45	38	31
14. *stammeri*	138	72	246	312	244	95	56	49	44
15. *byrrhidiphagus*	160	83	308	381	264	86	66	61	50
16. *lemae*	-	-	-	-	-	-	-	-	-

APPENDIX I. - continued.

Nominal species	Scape + radicle		Pedicel		Funicle article (no. sensory ridges)					
					1		2		3	
	L	W	L	W	L	W	L	W	L	W
1. *ovijentatus*	-	32	50	34	28	16	50	22	59	26(2)
2. *anomocerus*	-	26	44	31	20	14	27	17	41	23(2)
3. *perdubius*	-	26	46	29	20	14	35	14	48	16(2)
4. *alaskae*	169	40	72	41	35	24	74	25	65	32(1)
5. *behmani*	-	-	-	-	17	14	36	13	63	20(2)
6. *hercules*	153	-	-	-	-	-	-	-(1)	73	-(2)
7. *nigrellus*	146	31	55	28	24	17	60	21(1)	67	23(2)
8. *fuscipennis*	≈99	≈40	≈50	≈40	≈30	≈20	≈89	≈15	≈69	≈15
9. *pratensis*	-	42	69	34			118	19	104	19
10. *neopratensis*	-	-	-	38	36	19	130	17	106	18
11. *maculatus*	139	-	≈60	-	44	18	103	-	89	-
12. *filicornis*	-	38	66	35	32	-	109	18	95	17
13. *capitulatus*	108	30	51	30	34	19	74	15	66	14
14. *stammeri*	-	-	59	-	27	15	-	17	-	17
15. *byrrhidiphagus*	170	43	65	40	25	18	115	24	109	29(2)
16. *lemae*	108	24	48	28	33	21	48	16	66	24(2)
					24	15				

APPENDIX I. - continued.

Nominal species	Funicle article (no. sensory ridges)						Club	
	4		5		6		L	W
	L	W	L	W	L	W		
1. *ovijentatus*	57	30(2)	58	28(2)	61	31(2)	108	-(6)
2. *anomocerus*	30	20	42	22(2)	40	22(2)	86	28(-)
3. *perdubius*	39	16	50	20(2)	49	21(2)	93	30(6)
4. *alaskae*	67	33(1)	61	35(1)	64	39(2)	193	70(6)
5. *behmani*	62	20(2)	60	21(2)	56	21(2)	101	30(6)
6. *hercules*	77	-(2)	74	-(2)	68	-(2)	139	-(6)
7. *nigrellus*	68	23(2)	66	24(2)	66	24(2)	134	34(6)
8. *fuscipennis*	≈69	≈15	≈69	≈20(1)	≈59	30(-)	≈129	45(-)
9. *pratensis*	94	20	84	24(1)	75	34(2)	150	40(6)
10. *neopratensis*	90	19	82	25(1)	80	29(2)	154	58(6)
11. *maculatus*	80	-	76	-(1)	74	-(2)	143	-(6)
12. *filicornis*	88	19	83	22(1)	79	29(2)	148	46(6)
13. *capitulatus*	59	15	58	19(1)	58	23(2)	120	45(6)
14. *stammeri*	74	17	71	22(1)	70	30(2)	145	-(6)
15. *byrrhidiphagus*	100	27(1)	96	31(2)	90	35(2)	174	52(6)
16. *lemae*	67	25(2)	67	25(2)	68	24(2)	124	38(6)

APPENDIX II. Measurements (in µm) of primary types of nominal species of *Anaphes*. Abbreviations used: Fem.=femur; FW=fore wing; HT=holotype; HW=hind wing; L=length; LT=lectotype; Macro. dist.=distance between macrochaetae of marginal vein; ovip.=ovipositor; Stig.=stigmal vein; Tib.=tibia; Troch.=trochanter; W=width. Many measurements could not be made because parts were missing or not clearly visible. Measurements of structures positioned obliquely are not accurate, and are indicated by "≈". The holotypes of *A. amplipennis* and *A. pinguincornis* are lost.

Nominal species	Type	Head W	Mesosoma		Ovip. L.	Ovip./hind tibia
			W	L		
1. *medius*	HT	-	-	320	374	1.36
2. *ranalteri*	HT	-	-	298	315	1.30
3. *lacensis*	HT	-	-	298	337	1.48
4. *pectoralis*	LT	-	-	380	431	1.54
5. *wolfsthali*	HT	-	-	287	653	2.37
6. *hundsheimensis*	HT	-	-	236	340	1.60
7. *superadditus*	HT	-	-	275	216	1.00
8. *intermedius*	HT	-	-	332	349	1.23
9. *stubaiensis*	HT	173	-	225	316	1.92
10. *nunezi*	HT	272	230	389	614	1.91
11. *pucarobius*	HT	256	223	318	320	1.41
12. *neuquenensis*	HT	251	214	306	296	1.14
13. *fabarius*	LT	≈272	≈218	≈327	≈663	≈1.97

APPENDIX II. - continued.

Nominal species	FW				Total ven. L	Macro. dist.	Stig. L	Marginal space L
	L	W	L/W	LMC				
1. *medius*	≈782	156	5.01	137	254	69	32	111
2. *ranalteri*	767	142	5.42	148	239	57	38	128
3. *lacensis*	782	-	-	-	243	61	37	122
4. *pectoralis*	830	235	3.54	134	271	73	36	100
5. *wolfsthali*	906	186	4.87	235	294	87	41	574
6. *hundsheimensis*	614	104	5.92	108	206	53	32	81
7. *superadditus*	620	116	5.33	135	211	57	32	100
8. *intermedius*	823	149	5.52	143	254	68	32	127
9. *stubaiensis*	557	130	4.28	140	192	49	29	94
10. *nunezi*	1206	262	4.60	166	365	90	69	140
11. *pucarobius*	910	242	3.76	188	260	60	54	203
12. *neuquenensis*	935	229	4.08	178	267	64	55	197
13. *fabarius*	949	145	6.54	130	330	83	53	≈330

APPENDIX II. - continued.

Nominal species	HW			Ven. L
	L	W	LMC	
1. *medius*	759	-	-	234
2. *ranalteri*	737	31	127	230
3. *lacensis*	762	37	140	236
4. *pectoralis*	795	42	125	274
5. *wolfsthali*	827	35	160	253
6. *hundsheimensis*	599	19	93	202
7. *superadditus*	-	29	108	-
8. *intermedius*	815	31	130	269
9. *stubaiensis*	527	26	98	178
10. *nunezi*	1097	48	158	340
11. *pucarobius*	862	49	171	240
12. *neuquenensis*	868	44	164	244
13. *fabarius*	949	38	141	310

APPENDIX II. - continued.

Nominal species	Fore leg								
	Coxa	Troch.	Fem.	Tib.	Tarsus				
					Total	1	2	3	4
1. *medius*	-	-	174	170	170	51	43	43	33
2. *ranalteri*	≈92	41	165	157	162	52	43	37	31
3. *lacensis*	-	-	166	152	165	52	44	40	31
4. *pectoralis*	115	50	186	175	198	58	47	50	43
5. *wolfsthali*	-	-	-	-	≈201	-	-	-	-
6. *hundsheimensis*	78	41	136	133	132	38	33	32	29
7. *superadditus*	73	-	144	138	149	39	40	39	33
8. *intermedius*	105	41	183	181	174	52	45	41	33
9. *stubaiensis*	-	-	126	117	118	31	31	31	26
10. *nunezi*	-	68	-	-	215	61	56	59	41
11. *pucarobius*	-	-	182	177	150	-	-	-	-
12. *neuquenensis*	-	-	-	182	≈197	-	-	-	-
13. *fabarius*	-	-	-	≈198	≈210	≈50	≈40	≈40	≈50

APPENDIX II. - continued.

Nominal species	Middle leg								
	Coxa	Troch.	Fem.	Tib.	Tarsus				
					Total	1	2	3	4
1. *medius*	≈69	54	≈164	-	169	49	46	41	34
2. *ranalteri*	57	47	152	210	157	40	44	41	35
3. *lacensis*	≈59	≈46	≈148	-	≈168	≈41	46	41	-
4. *pectoralis*	74	53	182	239	183	47	50	50	35
5. *wolfsthali*	-	-	186	271	195	65	47	46	42
6. *hundsheimensis*	69	44	148	194	138	36	38	36	28
7. *superadditus*	49	47	146	191	154	39	34	41	32
8. *intermedius*	≈64	46	181	239	175	48	48	43	35
9. *stubaiensis*	49	-	≈128	158	104	22	27	29	26
10. *nunezi*	83	61	222	319	213	53	58	57	46
11. *pucarobius*	-	-	-	-	167	-	-	-	-
12. *neuquenensis*	-	-	-	≈237	179	≈48	≈46	≈46	38
13. *fabarius*	-	-	≈248	≈327	≈198	≈89	≈89	≈89	≈50

APPENDIX II. - continued.

Nominal species	Hind leg								
	Coxa	Troch.	Fem.	Tib.	Tarsus				
					Total	1	2	3	4
1. *medius*	109	-	197	271	≈176	50	46	44	35
2. *ranalteri*	108	62	190	245	165	44	46	41	34
3. *lacensis*	104	57	189	-	≈170	43	48	44	27
4. *pectoralis*	118	74	181	279	192	40	48	47	34
5. *wolfsthali*	-	-	-	-	≈175	46	49	43	38
6. *hundsheimensis*	97	≈53	171	212	140	35	39	37	30
7. *superadditus*	96	53	163	214	159	36	43	45	35
8. *intermedius*	108	68	212	280	181	49	50	47	35
9. *stubaiensis*	79	51	-	176	104	-	30	29	26
10. *nunezi*	127	71	278	330	222	49	64	63	46
11. *pucarobius*	118	-	229	258	165	-	-	-	-
12. *neuquenensis*	-	-	-	267	178	-	-	45	39
13. *fabarius*	-	-	-	≈337	≈218	≈50	≈59	≈50	≈40

APPENDIX II. - continued.

Nominal species	Scape + radicle		Pedicel		Funicle article (no. sensory ridges)					
					1		2		3	
	L	W	L	W	L	W	L	W	L	W
1. *medius*	-	33	57	33	28	17	70	18	78	23(2)
2. *ranalteri*	≈114	30	54	31	28	17	63	15	71	23(2)
3. *lacensis*	119	29	53	32	24	16	68	16	79	18(2)
4. *pectoralis*	118	-	56	34	29	17	69	20	74	27(2)
5. *wolfsthali*	-	35	68	32	34	16	105	17	89	19
6. *hundsheimensis*	106	28	48	25	24	13	51	15	59	21(2)
7. *superadditus*	≈92	22	43	24	22	14	60	16(1)	64	19(2)
8. *intermedius*	126	32	58	34	23	17	66	19	85	23(2)
9. *stubaiensis*	82	24	41	29	21	14	39	15	48	19(2)
10. *nunezi*	-	-	54	-	68	-	103	- (1)	105	- (1)
11. *pucarobius*	-	-	63	-	40	-	65	-	69	- (1)
12. *neuquenensis*	-	-	67	-	39	-	64	-	72	- (1)
13. *fabarius*	≈129	≈32	≈59	30	32	19	98	23(2)	104	25(2)

APPENDIX II. - continued.

Nominal species	Funicle article (no. sensory ridges)						Club			
	4		5		6		Total		1	2
	L	W	L	W	L	W	L	W	L	L
1. *medius*	75	25(2)	74	25(2)	72	25(2)	114	40(6)	n.a.	n.a
2. *ranalteri*	69	24(2)	65	24(2)	64	26(2)	113	38(6)	n.a.	n.a.
3. *lacensis*	79	24(2)	74	24(2)	67	25(2)	111	40(6)	n.a.	n.a.
4. *pectoralis*	72	30(2)	74	30(2)	66	30(2)	121	42	60(2)	59(4)
5. *wolfsthali*	76	24(1)	75	29(2)	69	29(2)	125	46	50(2)	80(4)
6. *hundsheimensis*	52	19(1)	56	22(2)	51	24(2)	95	32	38(2)	58(4)
7. *superadditus*	61	20(2)	64	21(2)	60	22(2)	113	31	49(2)	67(4)
8. *intermedius*	80	25(2)	75	27(2)	71	27(2)	120	41(6)		
9. *stubaiensis*	37	16	48	20(2)	45	22(2)	90	27	35(2)	55(4)
10. *nunezi*	92	- (1)	90	-(2)	88	-(2)	168	- (8)	n.a.	n.a.
11. *pucarobius*	71	- (1)	73	30(2)	67	32(2)	134	49(?7)	n.a.	n.a.
12. *neuquenensis*	71	- (1)	74	-(2)	66	-(2)	134	50(?7)	n.a.	n.a.
13. *fabarius*	95	26(2)	91	26(2)	≈79	≈20(2)	134	44(6)	60(2)	73(4)

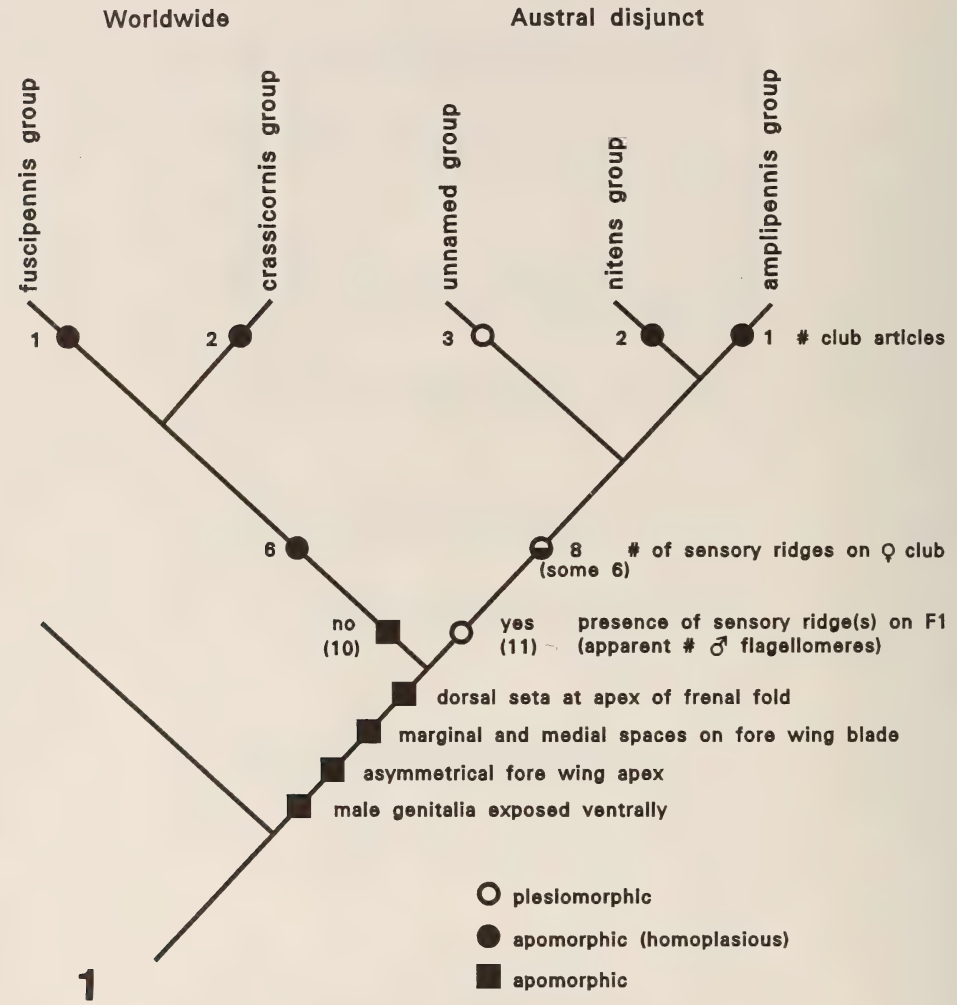
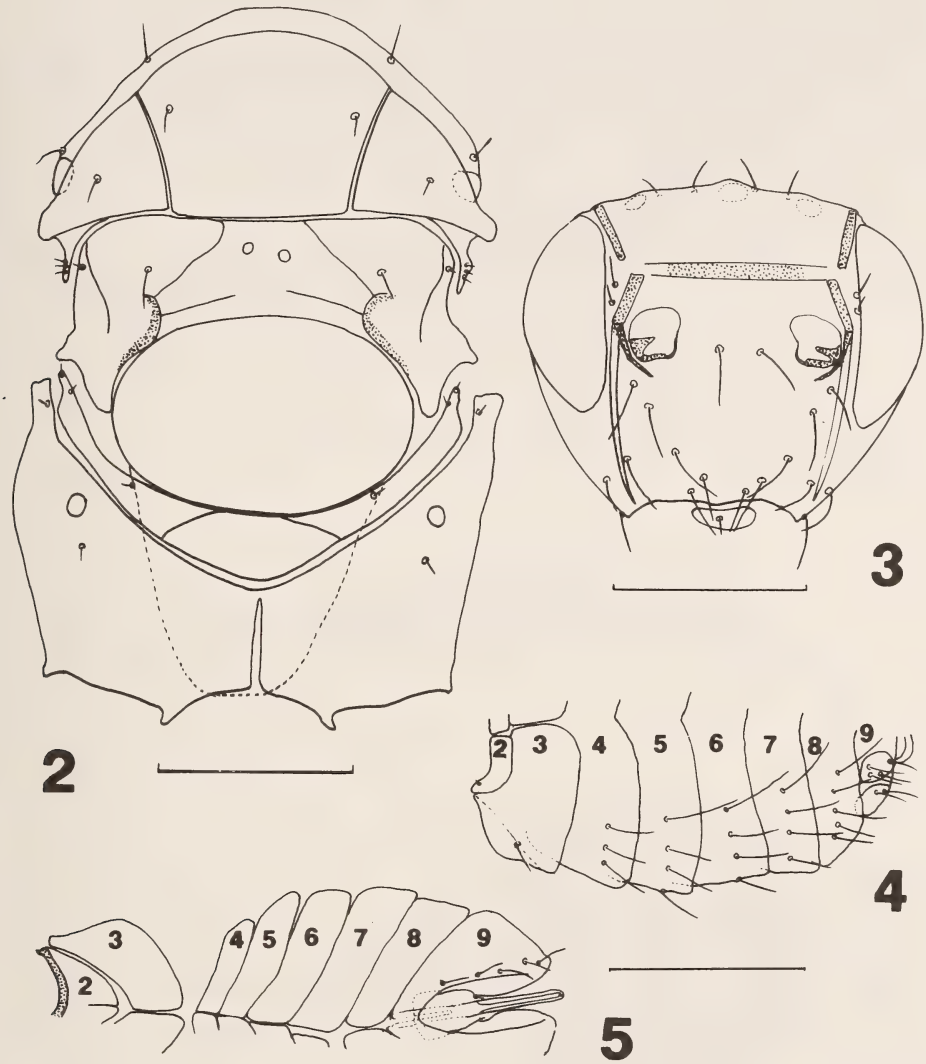
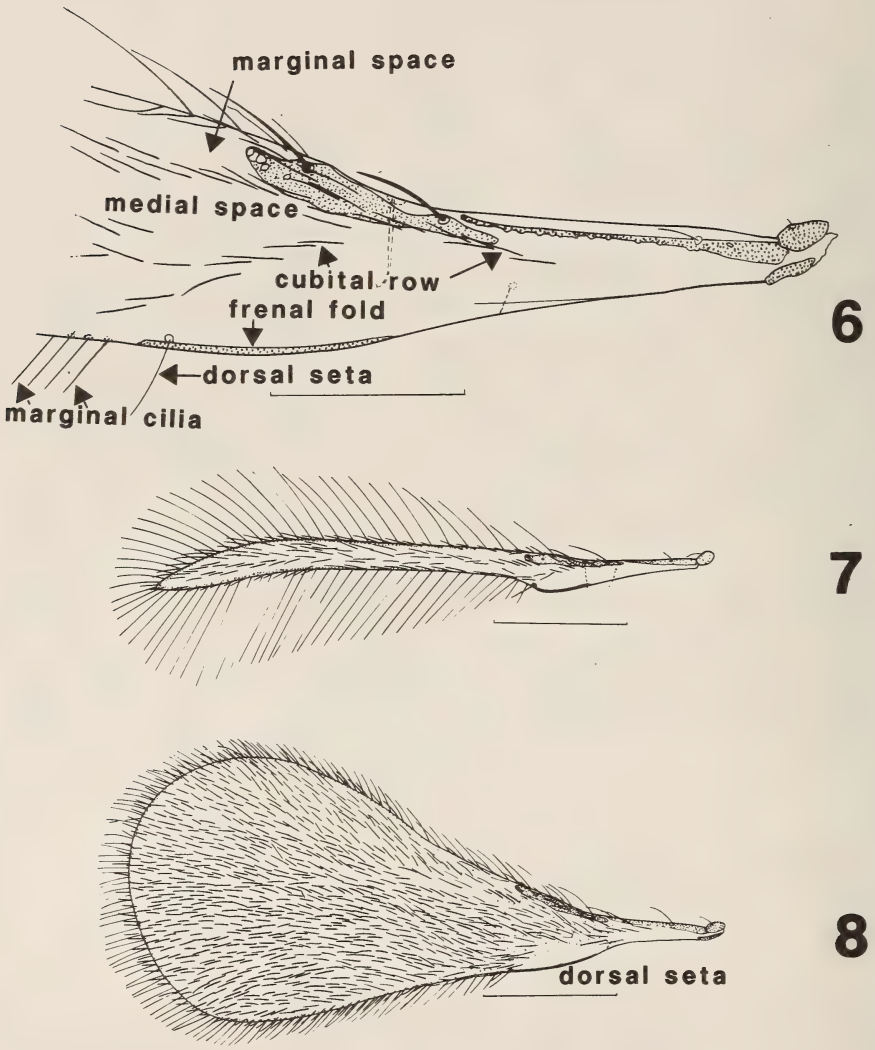


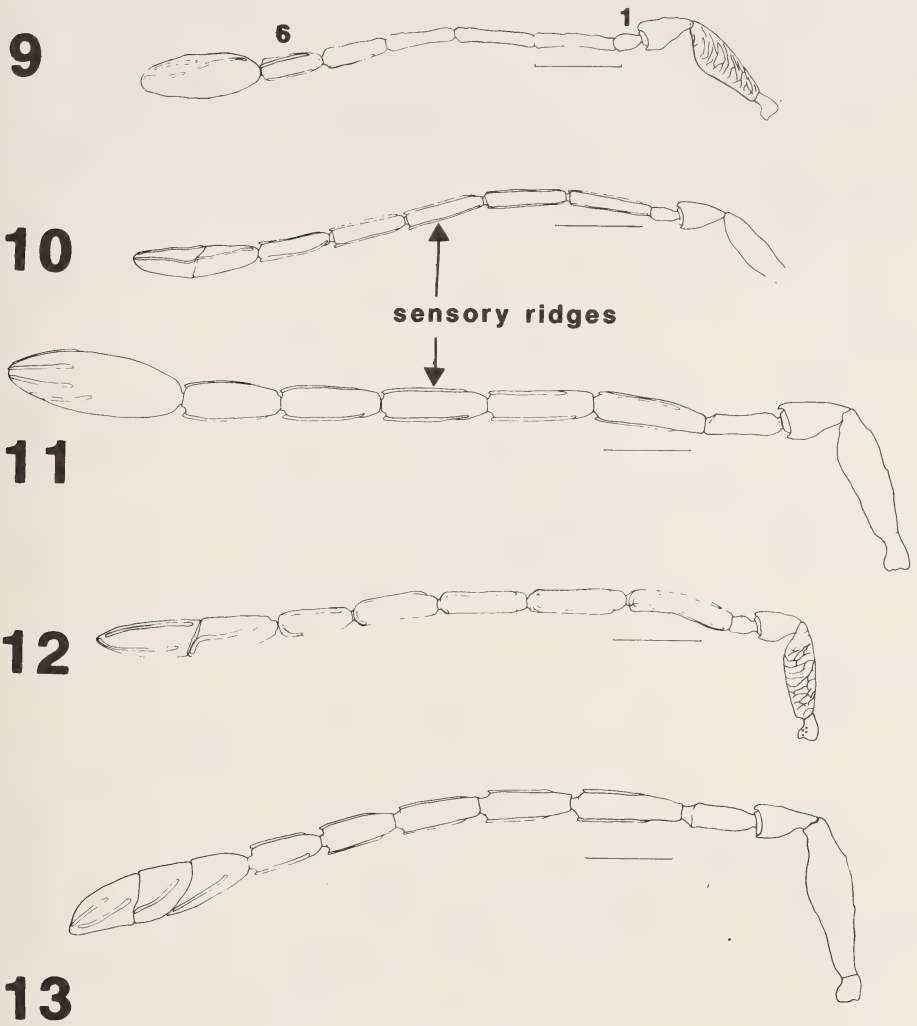
FIGURE 1. Cladogram showing relationships among species groups of *Anaphes* (Hymenoptera: Mymaridae) based on hypothesized apomorphies. See text for discussion.



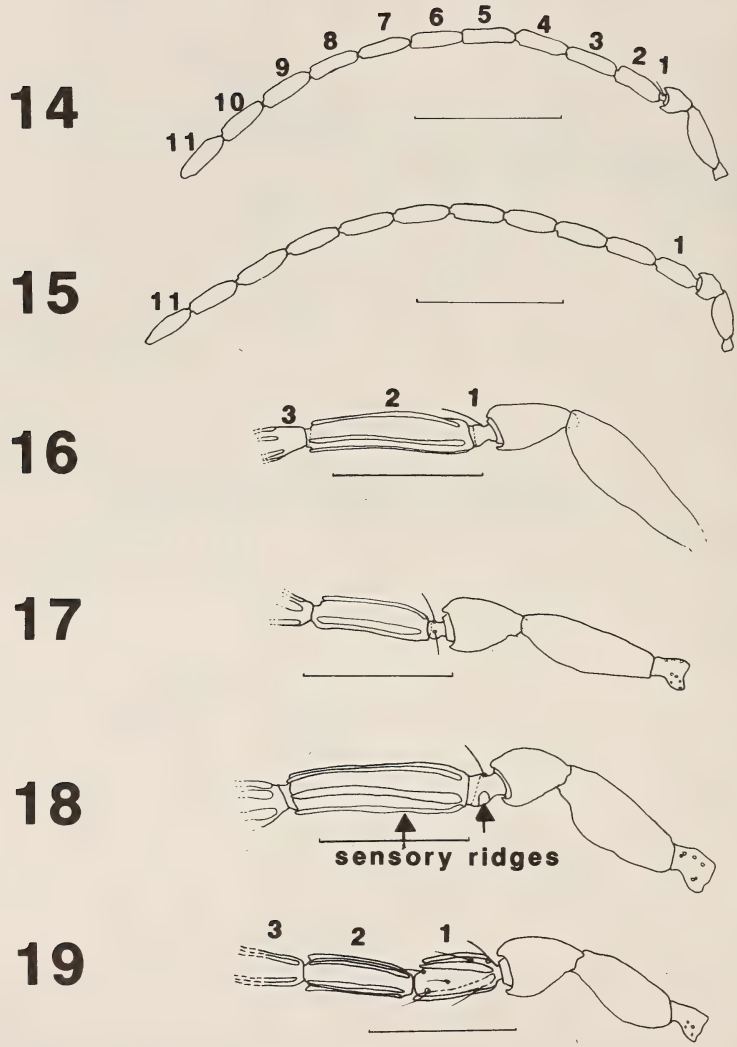
FIGURES 2-5. 2, *Anaphes fuscipennis*, mesonotum, dorsal view; 3, *Anaphes sinipennis*, head, anterior view; 4-5, *Anaphes byrrhidiphagus* allotype male, metasoma, 4, dorsal view, 5, ventral view (sternites 2 and 3 detached from remainder). Scale lines = 100 µm.



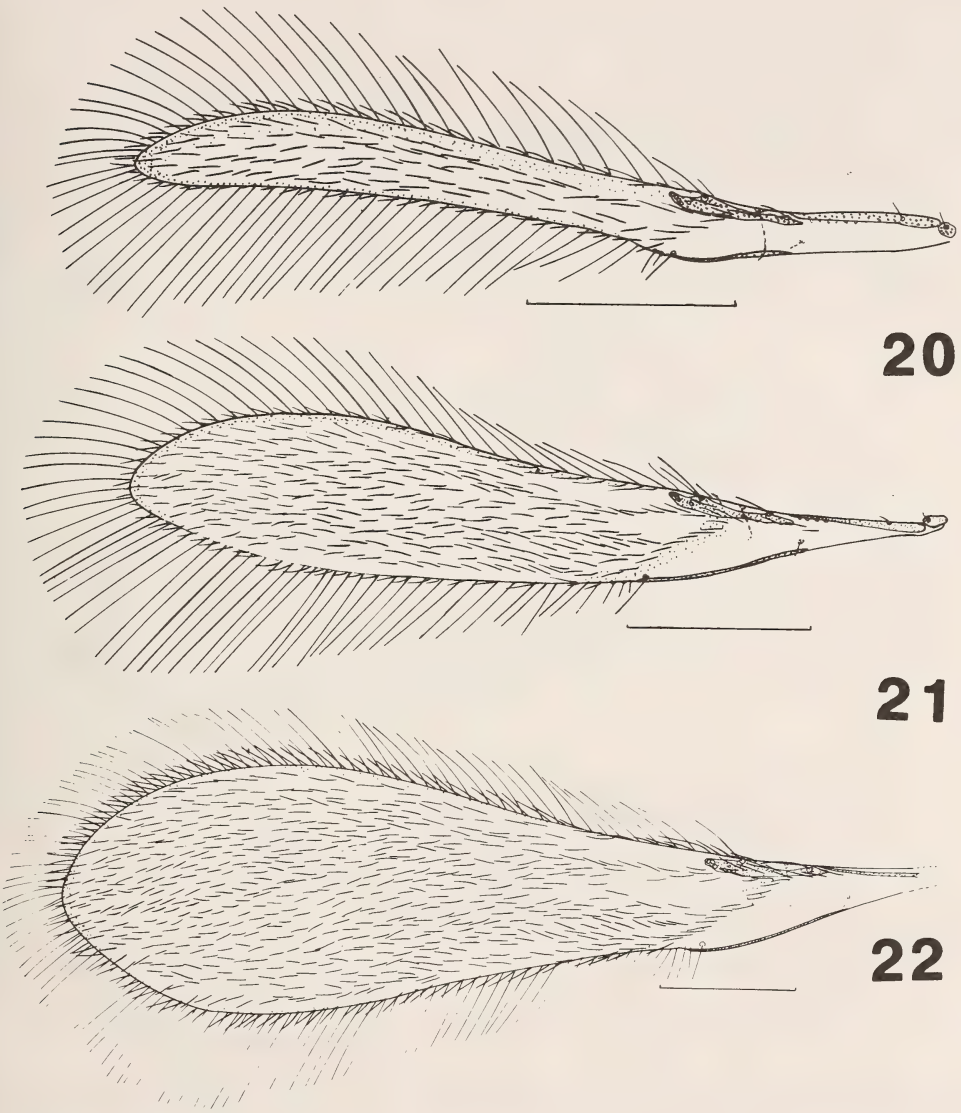
FIGURES 6-8. 6, *Anaphes fuscipennis*, base of fore wing, scale lines = 100 µm; 7-8, *Anaphes* spp. showing extremes of wing width: 7, *A.* sp. (Indonesia, Sulawesi, Utara, Dapau Mooat, Ketamobagu, V. 1985, J.S. Noyes); 8, *A.* sp. (New Zealand, AK, Titirangi, iv.1980, P.A. Maddison). Scale lines = 200 µm.



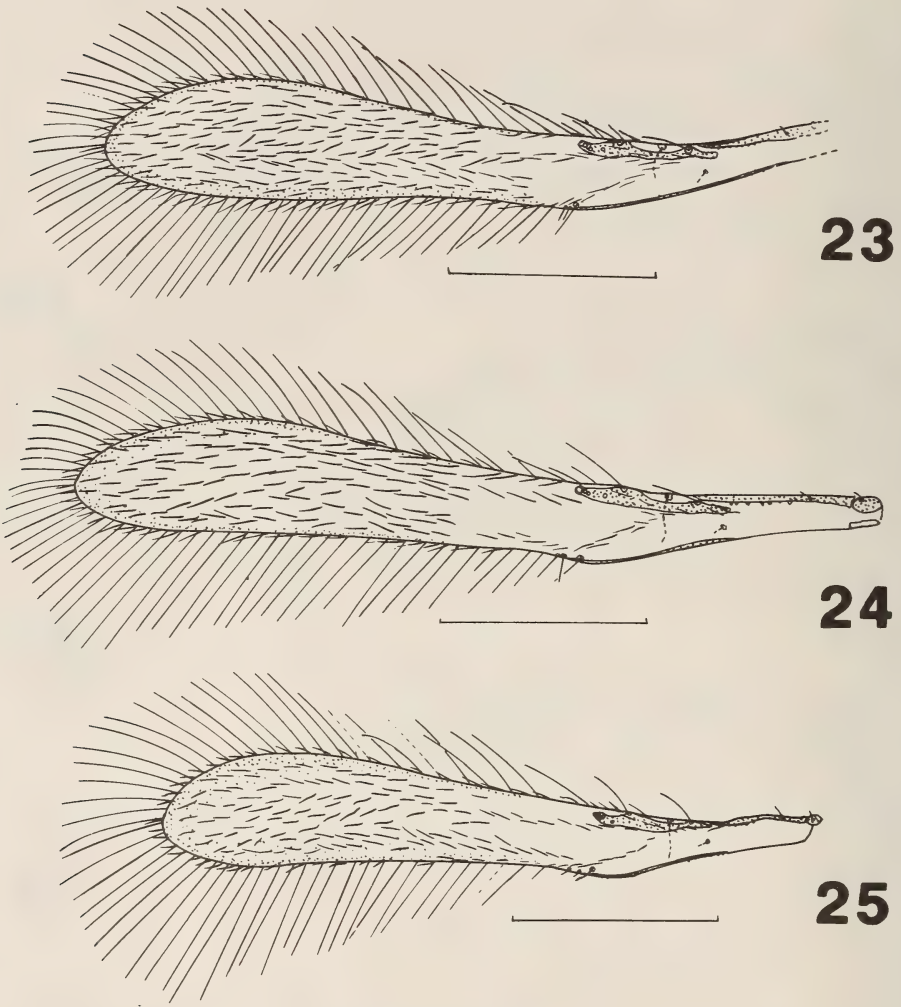
FIGURES 9-13. Female antennae of species from each species group of *Anaphes*: 9, *fuscipennis* group (*A. fuscipennis*); 10, *crassicornis* group (*A. acutiventris* Soyka, holotype); 11, *amplipennis* group (*A.* sp. ex. Chile, Aisen, 16 mi NW Cisnes Medio Rio Grande, 30.xii.1984-28.i.1985); 12, *nitens* group (*A. nitens*); 13, unnamed group (*A.* sp., New Zealand, Hokitika, Lake Mahinapua Res., 26-30.i.1978). Scale lines = 100 µm.



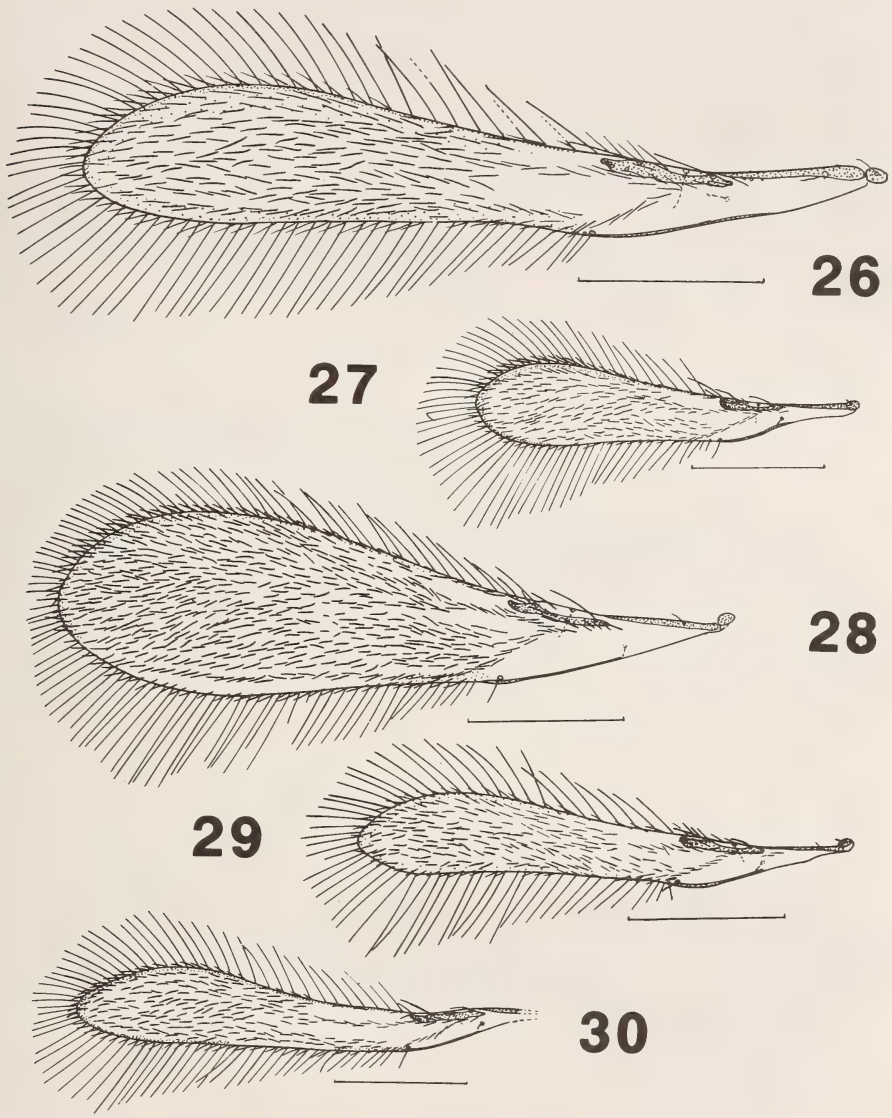
FIGURES 14-19. Male antennae of *Anaphes* spp.: 14, *A.* (*Anaphes*) *flavipes*; 15, *A.* (*Yungaburra*) sp. (Australia, New England National Park, 13.II.1984, L. Masner), scale lines = 200 µm; 16-19, basal segments of male antennae (scape to base of flagellomere 3): 16, *A.* (*Anaphes*) *acutiventris* Soyka; 17, *A.* (*Anaphes*) *fuscipennis*; 18, *A.* (*Yungaburra*) *nitens*; 19, *A.* (*Yungaburra*) sp. (*amplipennis* group, Chile, Princessa, 16.II.1985). Scale lines = 100 µm.



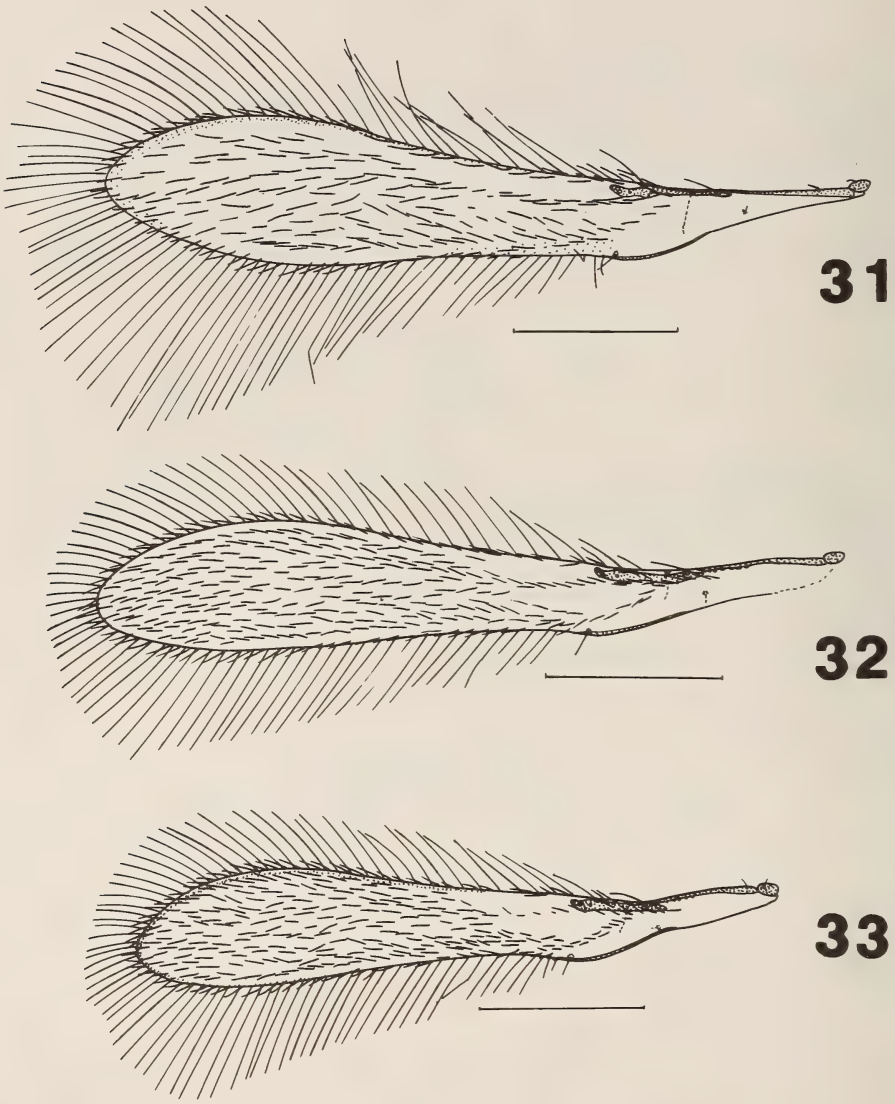
FIGURES 20-22. Fore wings of North American *Anaphes* spp.: 20, *A. sinipennis*; 21, *A. fuscipennis*; 22, *A. byrrhidiphagus*, holotype. Scale lines = 200 µm.



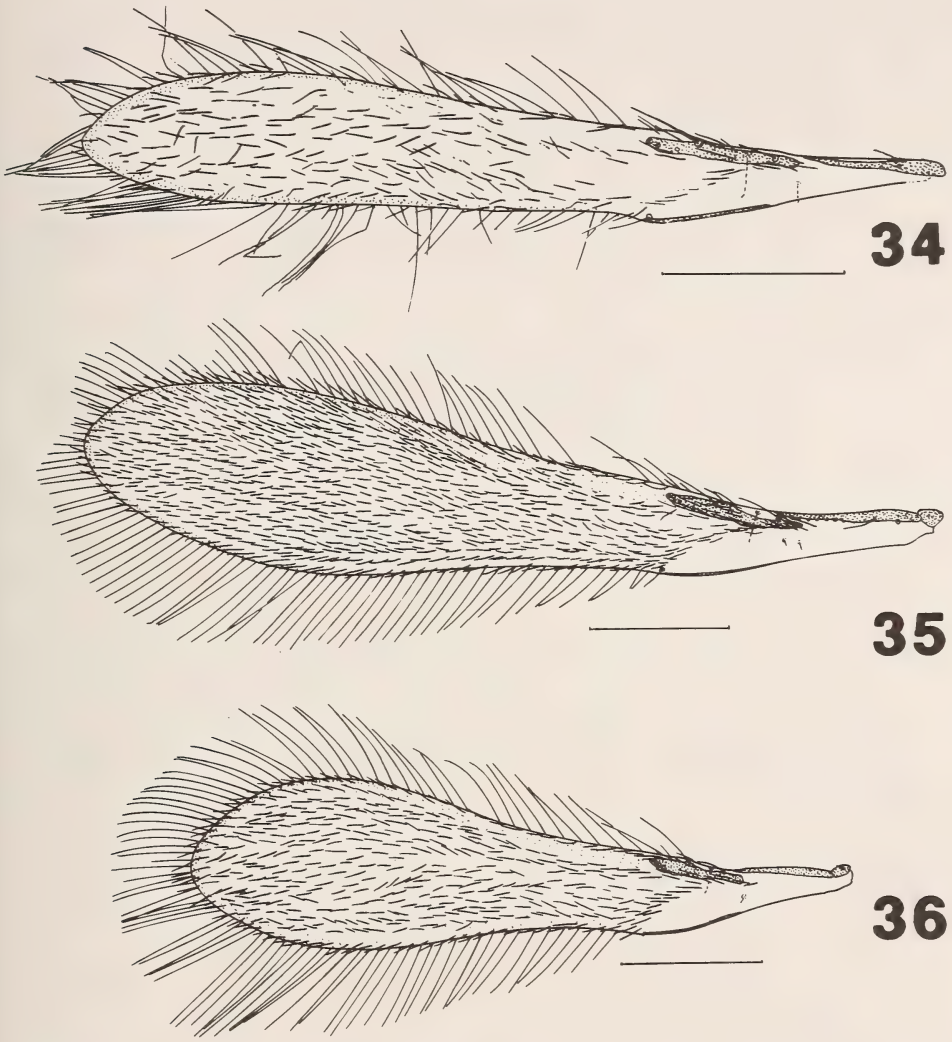
FIGURES 23-25. Fore wings of North American *Anaphes* spp.: 23, *A. nigrellus*, holotype; 24, *A. flavipes*, ex lab. culture from Niles, MI; 25, *A. behmani*, paralectotype. Scale lines = 200 µm.



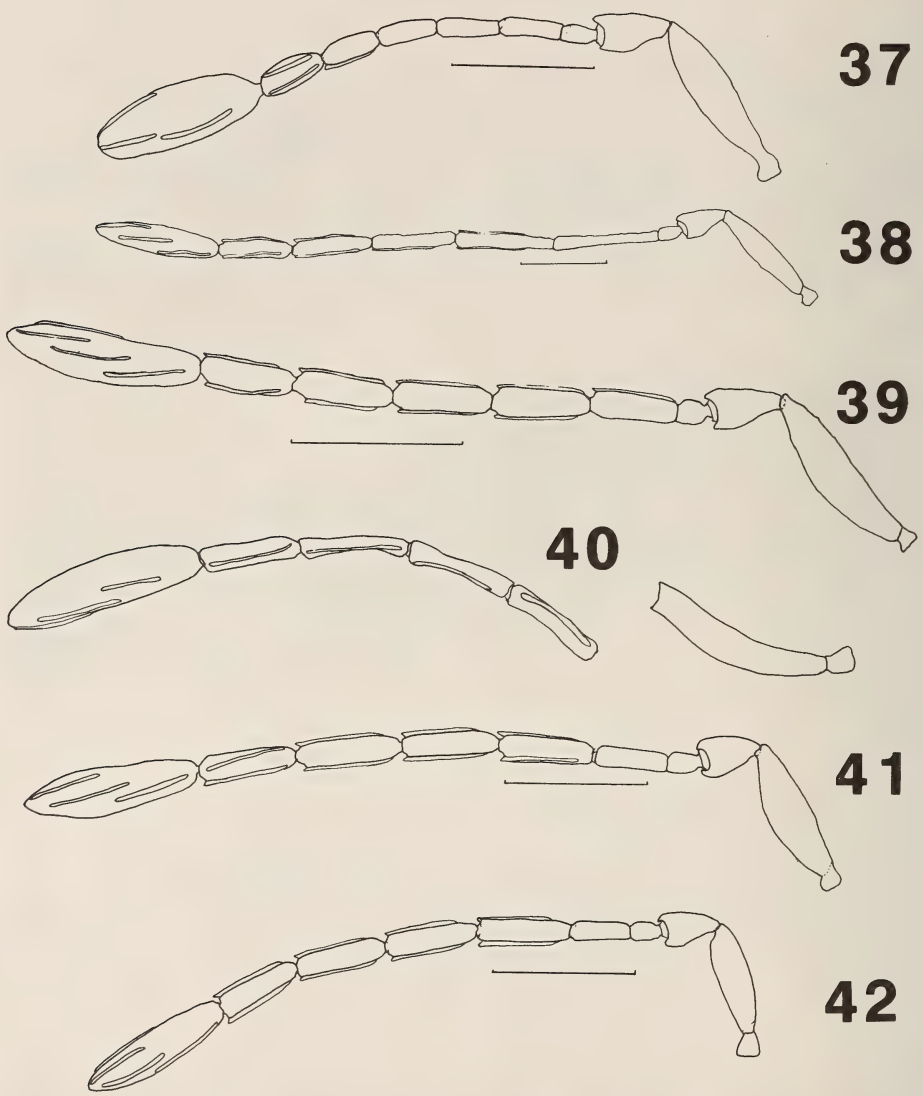
FIGURES 26-30. Fore wings of North American *Anaphes* and type species of various generic synonyms of *Anaphes*: 26, *A. hercules*, holotype; 27, *A. stubaiensis* (*Antoniella*), holotype; 28, *A. pectoralis* (*Hofenederia*), lectotype; 29, *A. hundsheimensis* (*Fulmekiella*), holotype; 30, *A. superadditus* (*Mariella*), holotype. Scale lines = 200 µm.



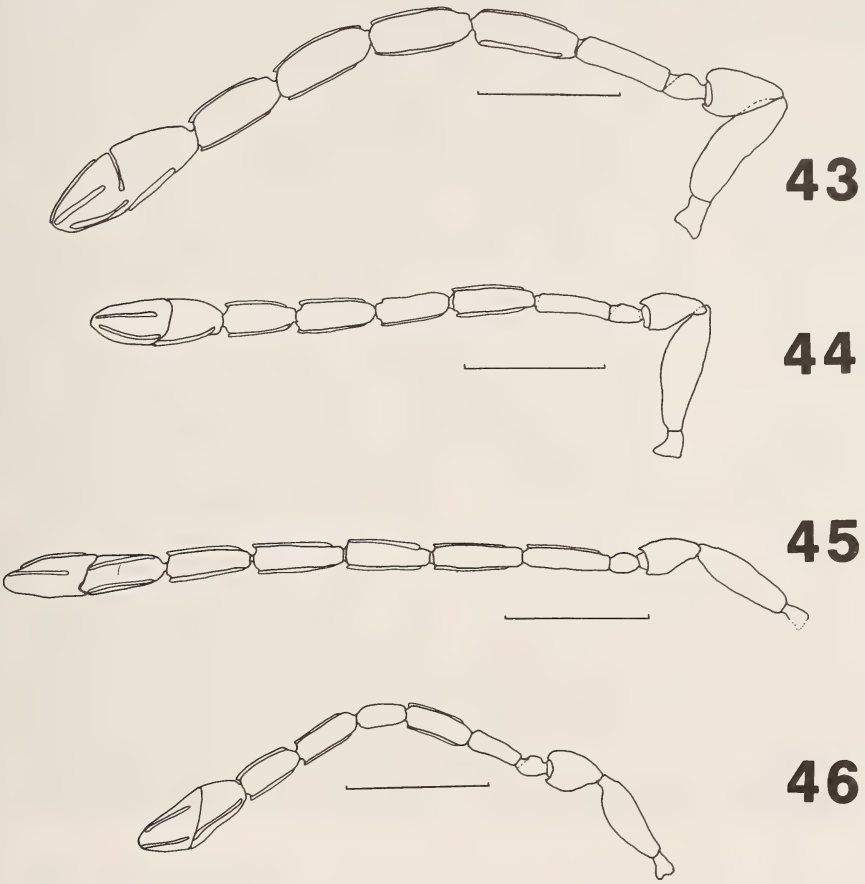
FIGURES 31-33. Fore wings of type species (except *A. ranalteri*) of various generic synomyms of *Anaphes*: 31, *A. wolfsthali* (*Stammeriella*), holotype; 32, *A. intermedia* (*Ferrierella*), holotype; 33, *A. ranalteri* (syn. of *A. medius*) (*Synanaphes*). Scale lines = 200 µm.



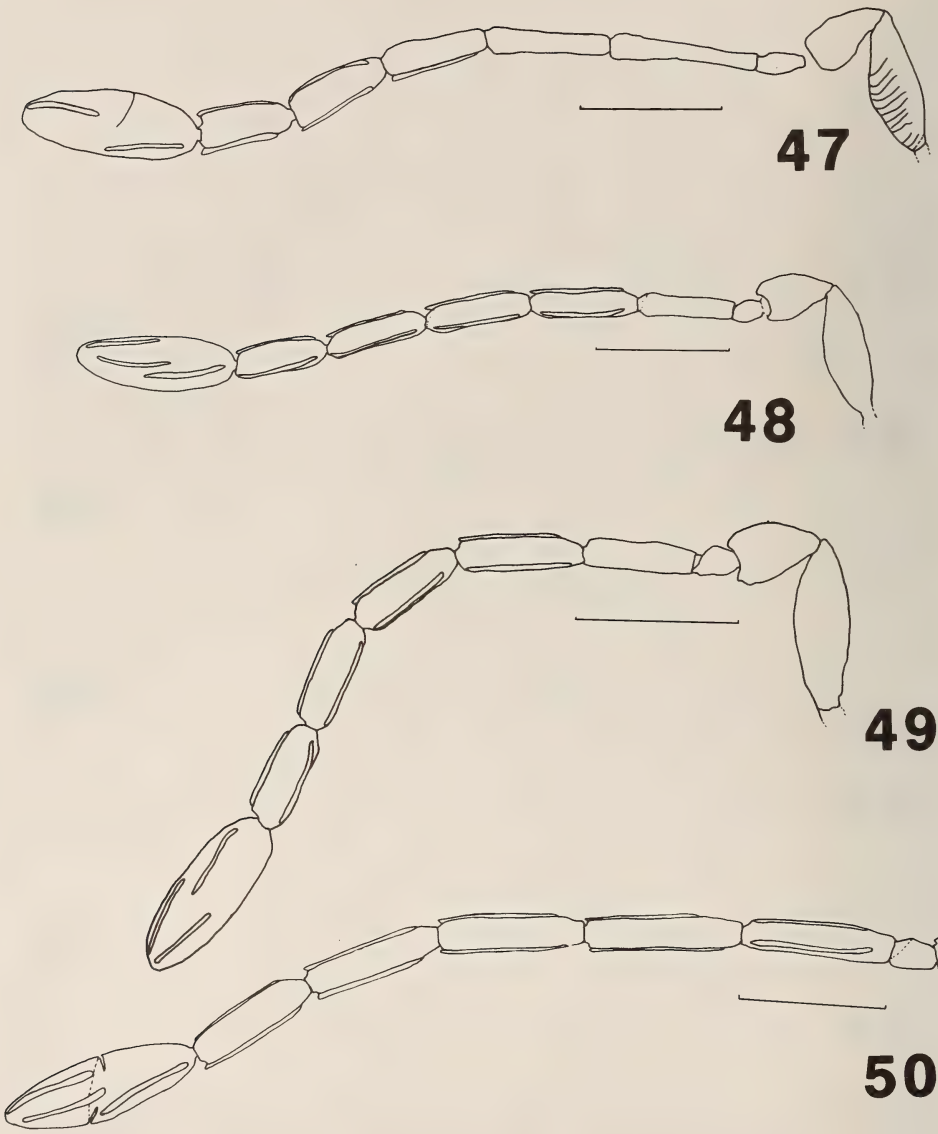
FIGURES 34-36. Fore wings of generic synomyms of *Anaphes* (*Anaphes*) and *Anaphes* (*Yungaburra*), *amplipennis* group: 34, *A. fabarius* (*Flabrinus*), lectotype; 35, *A. nunezi*, holotype; 36, *A. pucarobius*, holotype. Scale lines = 200 µm.



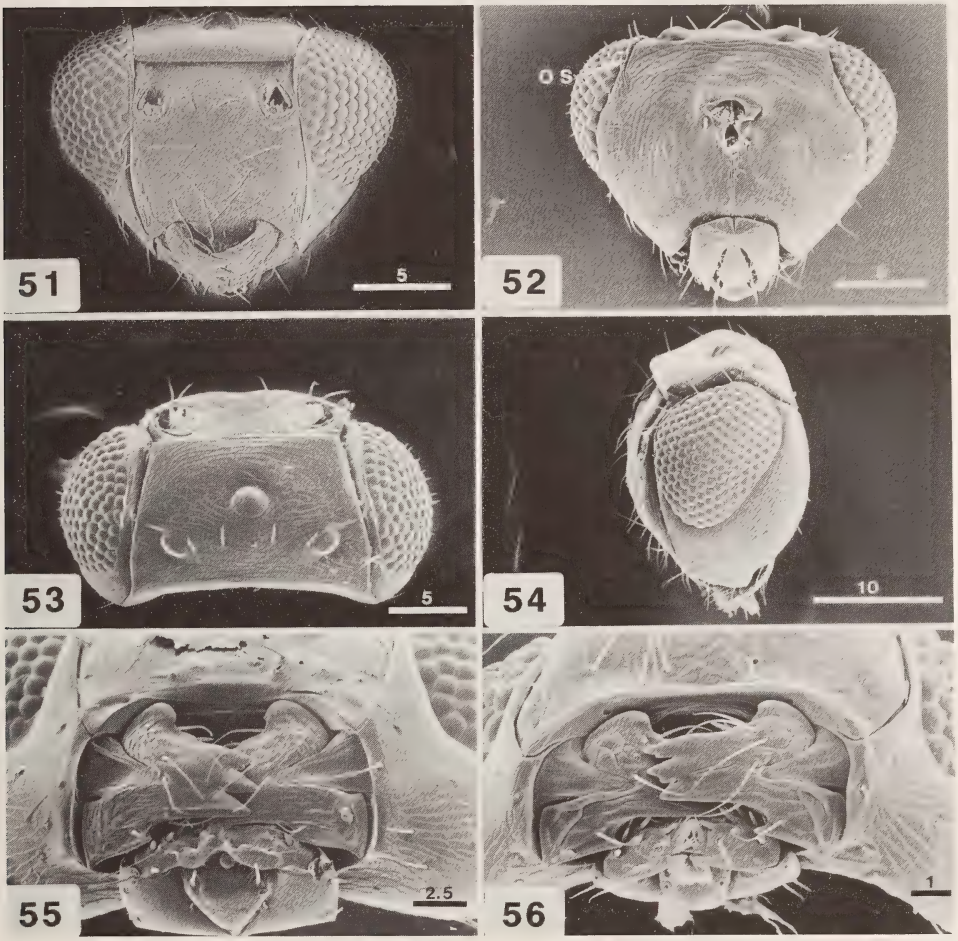
FIGURES 37-42. Female antennae of North American *Anaphes* spp.: 37, *A. sinipennis*; 38, *A. byrrhidiphagus*, holotype; 39, *A. nigrellus*, holotype; 40, *A. hercules*, holotype (scape in dorsal view, flagellomeres 1 and 2 not clearly visible; excluded); 41, *A. flavipes*, ex lab. culture from Niles, MI); 42, *A. behmani*, paralectotype. Scale lines = 100 µm.



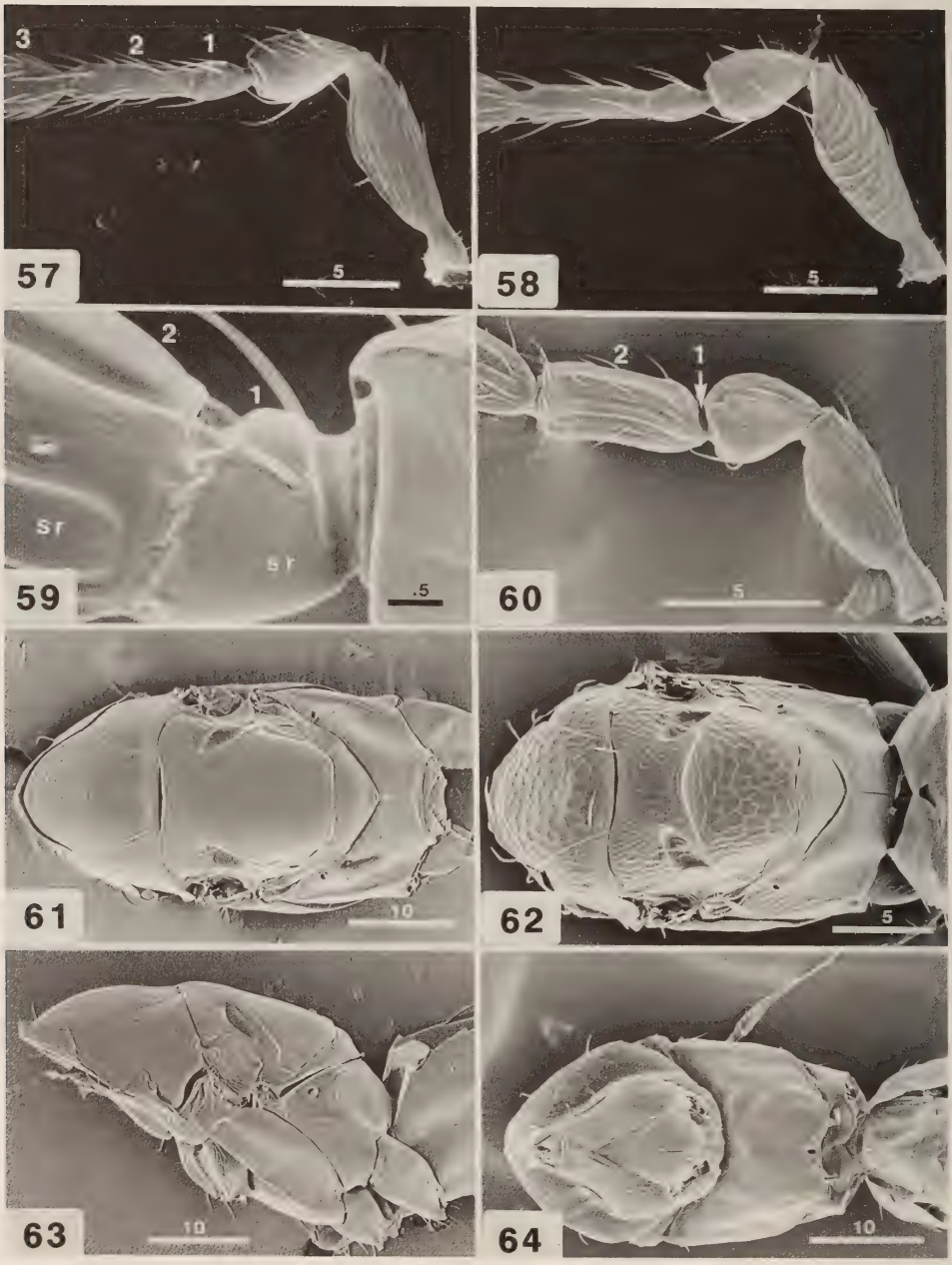
FIGURES 43-46. Female antennae of type species of various generic synomyms of *Anaphes*: 43, *A. pectoralis* (*Hofenederia*), lectotype; 44, *A. hundsheimensis* (*Fulmekiella*), holotype; 45, *A. superadditus* (*Mariella*), holotype; 46, *A. stubaiensis* (*Antoniella*), holotype. Scale lines = 100 µm.



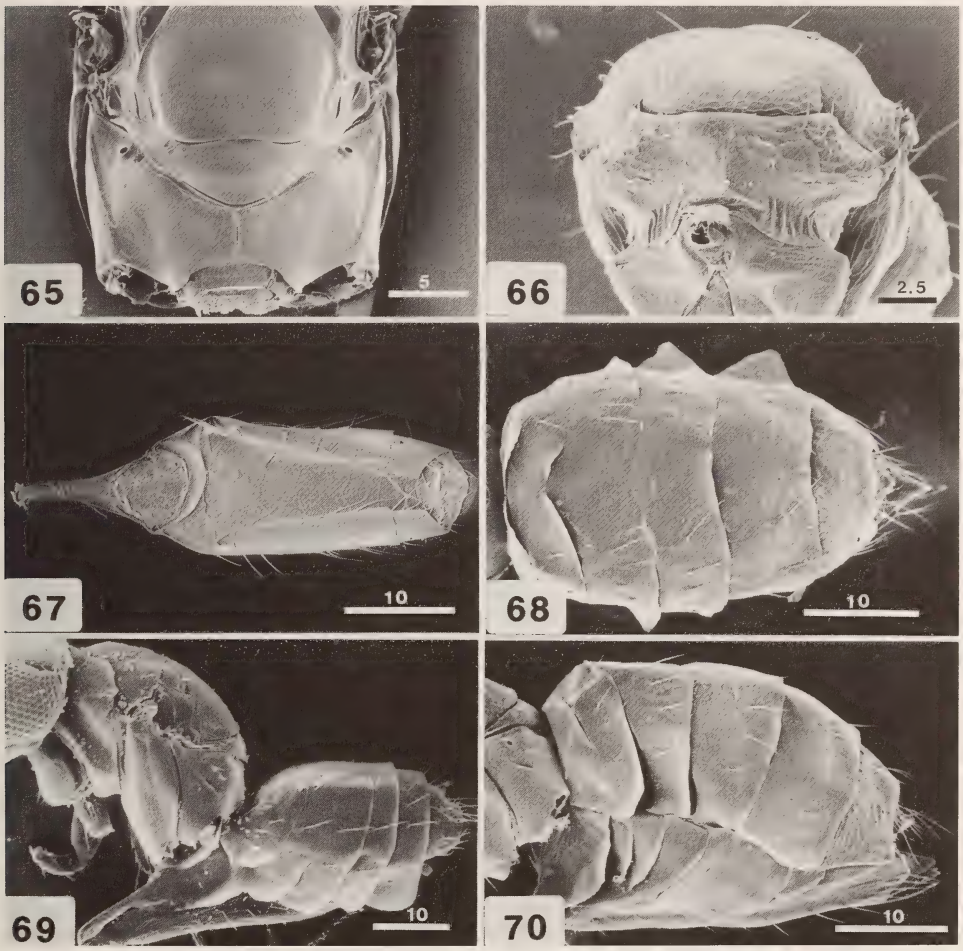
FIGURES 47-50. Female antennae of type species of various generic synomyms of *Anaphes*; 47, *A. wolfsthali* (*Stammeriella*), holotype; 48, *A. intermedia* (*Ferrierella*), holotype; 49, *A. medius* (*Synanaphes*) 50, *A. fabarius* (*Flabrinus*), lectotype. Scale lines = 100 µm.



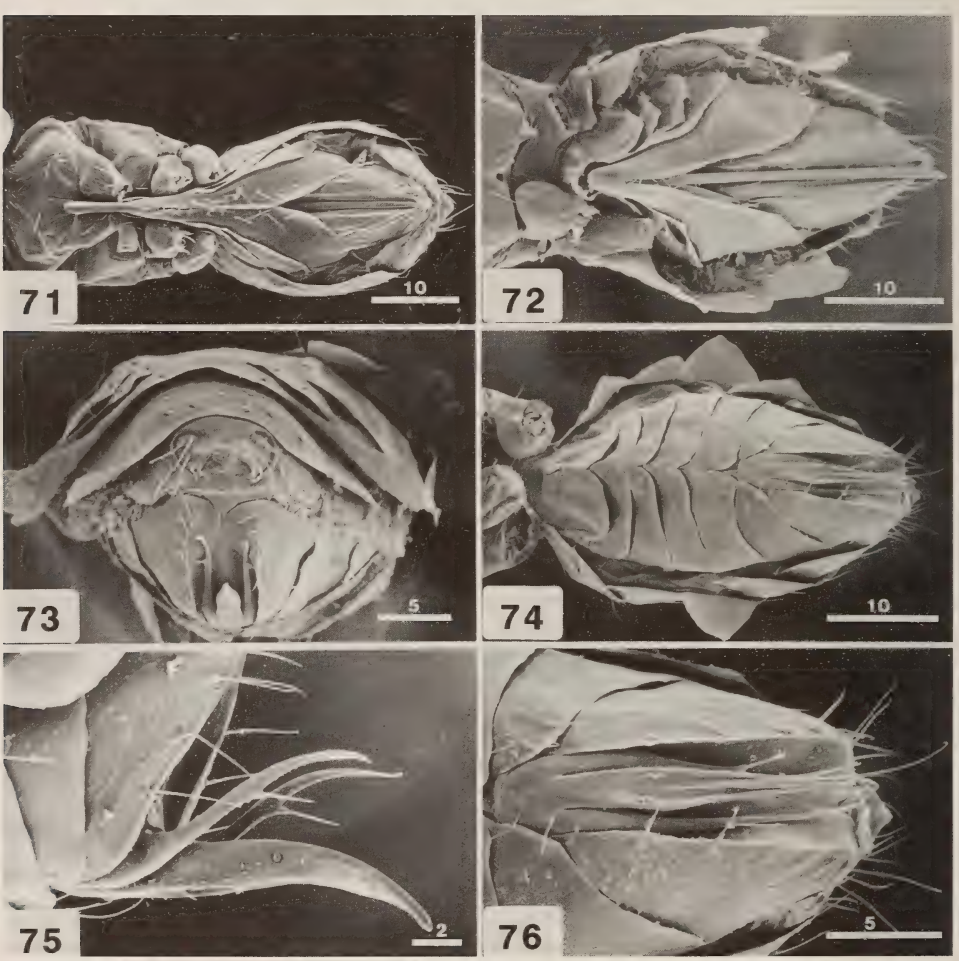
FIGURES 51-56. *Anaphes* spp.: 51, *A.* sp. (Indonesia, Sulawesi, Utara, Dapau Mooat, Ketamobagu, V. 1985, J.S. Noyes) head, anterior view; 52, head, posterior view (os = occipital suture); 53, *A. sordidatus* head, dorsal view; 54, *A. iole* head, lateral view; 55, *A. nitens* (Girault), mouthparts; 56, *A. diana* Girault, mouthparts. Scale lines x 10 µm.



FIGURES 57-64. *Anaphes* spp., female scape-base of F3: 57, *A.* ?*conotracheli* Girault, outer view, 58, *A.* ?*conotracheli*, inner view; 59, *A. nitens* (Girault), male apex of pedicel-base of F2 (sr = sensory ridge); 60, *A. iole* Girault, male scape-base of F3, outer view; 61, *A. nitens* (Girault) mesosoma, dorsal view; 62, *A.* sp. (ex. Sulawesi) mesosoma, dorsal view; 63, *A. nitens* (Girault) mesosoma, lateral view ; 64, *A. iole*, male mesosoma, ventral view. Scale lines x 10 µm.



FIGURES 65-70. *Anaphes* spp.: 65, *A. nitens* scutellum - propodeum, dorsal view; 66, *A.* sp. (ex. Sulawesi) mesosoma, anterior view; 67, *A. nitens* metasoma (collapsed), dorsal view; 68, *A. iole* female metasoma, dorsal; 69, *A. sordidatus*, female mesosoma + metasoma, lateral view; 70, *A. iole* female metasoma, lateral view. Scale lines x 10 µm.



FIGURES 71-76. *Anaphes* spp.: 71, *A.* ?*conotracheli*, female mesosoma + metasoma, ventral view; 72, *A. iole* female metasoma, ventral view; 73, *A. iole* male metasoma, posterior view; 74, *A. iole* male metasoma, ventral view, 75; *A. iole* male genitalia, lateral view; 76, *A. iole* male genitalia, ventral view. Scale lines x 10 µm.

THE BIOLOGY AND CONTROL OF THE TREFOIL SEED CHALCID, *BRUCHOPHAGUS PLATYPTERUS* (WALKER) (HYMENOPTERA: EURYTOMIDAE), IN ONTARIO

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Abstract *Proc. ent. Soc. Ont.* 123:111-122

The trefoil seed chalcid is widely distributed in seed fields of birdsfoot trefoil, *Lotus corniculatus* L. in southern Ontario. Overall levels of infestation averaged about 2 to 11.7% depending on the age of the fields, but were >50% in particular samples. In general, older fields were more severely infested than newly seeded fields. Unmanaged trefoil throughout Ontario supported one complete generation and a partial second generation of seed chalcids per year. Two hymenopterous parasitoids, *Mesopolobus bruchophagi* (Gahan) and *Aprostocetus bruchophagi* (Gahan), parasitized the trefoil seed chalcid but parasitism was only 8.2 and 11.0%, respectively. *A. bruchophagi* began to emerge earlier than its host, and cumulative emergence was too early to be well synchronised with seed chalcids in the field.

Pre-bloom sprays of dimethoate were ineffective because their application occurred before significant numbers of chalcids emerged on the first growth, and before populations peaked on the regrowth. In general, the level of infestation in seeds collected from regrowth trefoil (19.1%) was about five times that in seeds from the first cut. Because populations of chalcids increased throughout the season, shifting the seed crop to the first cut would significantly reduce the infestation of seed by chalcids. Destroying screenings from seed cleaning, reducing the amount of volunteer trefoil near seed fields, and locating new fields away from old ones are important for reducing infestations.

Introduction

Seed chalcids (Hymenoptera: Eurytomidae) are important pests in most countries that produce alfalfa, clover or trefoil seeds (Neunzig and Gyrisco 1958; Batiste 1967). The biology of the trefoil seed chalcid, *Bruchophagus platypterus* (Walker), was described by Batiste (1967). Adults lay their eggs in new, soft seeds during the summer, and larvae then feed within them leaving hollow non-viable seeds by the time they pupate. Seed losses have ranged from 5 to 85% (Kolobova 1950; Strong 1960; Romahkow 1968; Harpaz 1978; Prashar and Dhaliwal 1984).

Control with insecticides is difficult because insect pollination is indispensable for seed production, and trefoil is an indeterminate bloomer which can flower for nearly two months. Thus, it is difficult to control chalcids attacking the new pods without poisoning the necessary pollinators. Several species of parasitoids attack chalcids (Butler and Hansen 1958; Neunzig and Gyrisco 1959) and these could also be destroyed by sprays. Although Dochkova *et al.* (1982) claimed control without harming bees, and some success was reported on red clover in Hungary (Perju 1982) and on alfalfa in USSR (Antonova and Bazyleva 1974), no insecticides are registered for this purpose in Canada. Perhaps if chalcids are numerous in the fields before bloom, a short-residual, pre-bloom spray would be effective without harming beneficial insects.

A sizeable complex of parasitoids attacks seed chalcids (Neunzig and Gyrisco 1959). In addition, a comprehensive program of cultural controls has been recommended (Dochkova *et al.* 1982). Cultural controls include destroying volunteer host plants from wastelands, delaying the period of pod set (Batiste 1967; Harpaz 1978), and destroying waste material produced during seed cleaning. The extent of parasitism and the possibility of cultural control has never been addressed for Ontario trefoil fields.

Our objectives were to determine the extent of the chalcid problem on trefoil in Ontario, the seasonal population trends of the seed chalcid and its parasitoids, and the possibility of control with insecticide and by cultural means.

Materials and Methods

Survey for Trefoil Seed Chalcid and its Parasitoids

A survey of seed fields was carried out near the town of Cayuga (43°N.) in Haldimand-Norfolk County, southern Ontario, in August and September 1988. Samples of 50 mature umbels (pod clusters) were randomly collected from each of 33 trefoil fields. These fields had been in trefoil seed production for periods ranging from 1 to over 10 years. The umbels were transported to the laboratory in paper bags, held for one month to dry, and then threshed in a hand-operated, rubber-lined rotary thresher. The seeds were partly cleaned by shaking them over a series of screens to remove debris, and further cleaned using an air-stream seed cleaner which was regulated to remove the chaff without losing seeds.

The clean samples were stored at 0°C for 12 weeks to break the diapause of chalcids and parasitoids. The samples were then placed in cages and held in a growth chamber at 24 ± 2°C, with 16:8h (L:D) photoperiod. Emerging insects were counted daily and preserved in 70% alcohol. Chalcid and parasitoid species were identified by the Biosystematics Research Centre, Ottawa.

Determining Percent Infested Seed

When all insects had emerged, seven lots of approximately 100 seeds were taken from every sample and used to estimate the level of chalcid infestation. Each sample was emptied into a polyethylene bag, and a flat Plexiglass® slab (25 x 5 cm) bearing 100 equally-spaced depressions was slid into the bag to remove seeds following the technique of Strong (1960). Seeds were then lifted from the slab by placing a strip of adhesive tape over the sample. Another strip of tape was added, to sandwich the seeds. Seeds were crushed in the strips of tape with a wooden roller, and then sound, shrivelled and chalcid-infested seeds were counted. Sound and shrivelled seeds remained intact whereas hollow, infested seeds were cracked open.

Seasonal Population Trends

A weekly programme of sweep sampling for adult chalcids and parasitoids was conducted on three trefoil fields and an area of unmanaged roadside trefoil in Haldimand-Norfolk County, and on two trefoil fields near New Liskeard (47.5°N), northern Ontario. None of the areas was sprayed with insecticide during the study. Twenty-five sweeps with a 38-cm-diameter sweepnet comprised a sample. In southern Ontario, four samples were taken per field while walking an M-shaped pattern, whereas three samples per field were taken in the New Liskeard area. Insects were preserved in 70% alcohol until chalcids and two species of parasitoids could be counted with the aid of a dissecting microscope.

On each sample date, twenty trefoil plants were randomly selected per field. These plants were used to classify the morphological stage of trefoil development as vegetative, bloom, or pod using a modification of the method Kalu and Fick (1981) used on alfalfa.

During pod set, the number and colour of umbels were also noted, and one light brown umbel was randomly removed from each of the twenty plants. These umbels were later dissected under a binocular microscope to record the numbers of larval chalcids and parasitoids in infested seeds.

In September 1989, most pods had matured and were brown. A random sample of 50 umbels was taken from each field and threshed to obtain clean seeds which were later used for estimating percentage of chalcid infestation by the methods previously described.

Effect of Pre-bloom Sprays on *B. platypterus*

In 1989, four separate seed fields in Haldimand-Norfolk County were used to evaluate pre-bloom foliar sprays of dimethoate on both the first-cut seed crop and the regrowth crop. A 50 by 50 m area in each field was subdivided into two plots each measuring 50 by 25 m. One plot was sprayed with dimethoate and the other was left to serve as a non-sprayed control plot. When hay was cut in June, half the sprayed and non-sprayed areas of each field were left uncut to produce the first-cut seed crop, and the other half was clipped and seeds were produced on the regrowth. The first-cut crop was sprayed in the spring while the regrowth was sprayed during summer. Dimethoate spray was applied through 8002 flat-fan nozzles at a pressure of 275 KPa at the rate of 0.2 kg AI in 225 L of water per ha. Populations of adult seed chalcids were estimated in every plot from four samples, each consisting of twenty-five sweeps, using a 38-cm-diameter net. The samples were taken before treatment, and at 2, 5, and 12 days after treatment.

In September 1989, samples of mature pods (umbels) were taken from every plot on both the first cut and on the regrowth for determining percentage of infested seeds. This study used a 2 by 2 factorial design for investigating the percentage of seeds infested in the two growth periods when the trefoil was either sprayed or left non-sprayed. Two-way ANOVA (SAS Institute 1987) was used to determine the effect of growth periods (spring and summer) and dimethoate sprays on the percentage of seeds infested by chalcids in the field.

Spread of *B. platypterus*

Studies were carried out at two sites to determine the spread of trefoil seed chalcids from old fields into newly cultivated trefoil fields. At each site, an old field, which was seeded eight years ago, was located beside a new field, seeded in 1988. Two samples of 50 sweeps each were taken from an old trefoil field, and then at 50, 100 and 150 m from the bordering edge into a neighbouring new field. Sampling was carried out in the last week of each month, from May to August 1989. In September 1989, a random sample of 50 brown umbels was taken at each location and used for determining percent seed infestation at the end of the growing season. The two sites represented blocks while locations represented treatments. ANOVA (SAS Institute 1987)

was used to determine if the number of adults collected at various locations was different, and if infestation levels in the seeds were different.

In another experiment, about two kilograms of screenings were scooped from a dumpsite located at Canfield, Ontario in May 1990. Screenings usually contain small and broken seeds, infested seeds, and chaff (Winch *et al.* 1985). The screenings were subdivided into ten lots of 21 g and the rest discarded. Each lot was placed in an emergence cage and stored in a growth chamber at 27 ± 2°C, 50% R.H., 16:8h (L:D) photoperiod. The cages were inspected daily and the *B. platypterus* that emerged were counted and recorded.

Results and Discussion

Occurrence of *B. platypterus*

Bruchophagus platypterus was widely distributed and emerged from every sample of seeds collected from commercial fields (Table I). The percentage of infested seeds ranged from <1 to about 20%, with older fields more likely to have larger infestations. Infestation in fields greater than five years old (11.9 ± 2.17 S.E.) was significantly greater than in younger fields (2.6 ± 0.43 S.E.) ($F = 10.74$, df = 9,23, $P = 0.01$). Antonova and Bazyleva (1974) in the USSR and Dughetti (1985) in Argentina also found higher chalcid infestations in older fields.

Inevitably, pods shatter during harvest and scatter infested seeds in the field. However, the relationship between years in seed production and infestation levels is complicated by several factors. Sometimes seed crops in Ontario are not harvested because of poor growth or weather conditions. Such crops drop all their seeds, and the following year they may experience higher chalcid infestations like those reported on uncultivated trefoil by Batiste (1967). Alternatively, the farmer may decide to harvest the entire crop of trefoil as hay in a particular year. When this occurs, few or none of the seeds mature to drop in the field, and the population of seed chalcids may return to levels typical of a first-year field. Thus, even though on average younger fields are less heavily infested than older fields, it was inappropriate to calculate a regression equation of infestation versus years in seed production because the above factors were not determined.

Occurrence of Parasitoids

Two species of parasitoids, *Aprostocetus* (=*Tetrastichus*) *bruchophagi* (Gahan) (Hymenoptera: Eulophidae) and *Mesopolobus* (=*Amblymerus*) *bruchophagi* (Gahan) (Hymenoptera: Pteromalidae), were recovered from samples of infested seed (Table I), but not from all the fields. Emergence from 320 infested seeds held singly in clear capsules confirmed that only one parasitoid emerged per infested seed. *A. bruchophagi* emerged from seeds from about 47% of the fields, and *M. bruchophagi* from 38% of the fields, while neither species was recovered from some fields. The two species of parasitoids of trefoil seed chalcid that we found in Ontario were the two most abundant species reported in Wisconsin (Peterson *et al.* 1992a) and among the five reported from New York State (Nuenzig and Gyrisco 1959). *A. bruchophagi* was also the most important species on trefoil seed chalcid both in New York (Nuenzig and Gyrisco 1959) and in California (Batiste 1967).

Older fields were more likely to contain hosts with parasitoids than were younger fields (Table I). This relationship was expected because seeds with hosts were generally more numerous in older fields (increasing the probability of recovery), and hosts must establish before their parasitoids.

TABLE I. Infestation by *B. platypterus* and its parasitoids in trefoil seed from 33 commercial Ontario fields in 1988.

Years in trefoil[1]	Number of fields	Average infestation[2] (% of seed)	Percentage of fields					
			B. platypterus infestation (% of seed)				Parasitoid	
			0	<1	1-5	>5	*Aprostocetus bruchophagi*	*Mesopobolus bruchophagi*
2	10	2.8 a	0	40	50	10	50	20
3-5	14	2.4 a	0	0	93	7	14	43
>5	9	11.9 b	0	0	22	78	89	55

[1] Two years in trefoil means the first year of seed production following seeding the previous year.

[2] Means followed by the same letter are not significantly different using Duncan's multiple range test ($P = 0.05$).

Seasonal Population Trends

Trefoil seed chalcids were first detected in fields of southern Ontario in late May when the crop was still in the bud stage (Fig. 1A, B and C). Populations increased to about 20 insects/100 sweeps by July and then declined to about 5 insects/100 sweeps following cutting of the hay. Thereafter, numbers rose again and reached a peak on the regrowth by mid-August at over 100 insects/100 sweeps. Thus, the number of chalcids increased as the season progressed, and peak populations coincided with the period of pod set in the field. These results agree with those found for *B. roddi* in the southern Great Plains (Nielson 1976; Ahring *et al.* 1984; Thoenes and Moffett 1990).

On roadside trefoil in southern Ontario (Fig. 1D), adults increased uninterrupted and in June reached a peak of about 150 insects/ 100 sweeps. A decline in mid-July was attributed to part of the trefoil being cut to improve visibility along the road. A second generation of chalcids was confirmed by the presence of exit holes in some pods, and resulted in a second peak of adults in the middle of August. The chalcid population declined again in late August, probably due to emigration because there were no more green pods on the wild trefoil. According to Batiste (1967), these emigrating chalcids often end up in neighbouring trefoil fields.

Fields in northern Ontario were not cut for hay before allowing the crop to mature seeds. Chalcids first appeared in the field in late June, and maintained at low densities of about 5 insects/100 sweeps until late August when a modest peak occurred (Fig. 1E). As in southern Ontario, this August peak occurred during pod set. The coincidence of chalcids with pods in the field led to ideal conditions for oviposition by *B. platypterus*, but because of the short growing season, only a partial generation emerged as was confirmed by the presence of a few exit holes on trefoil in late August.

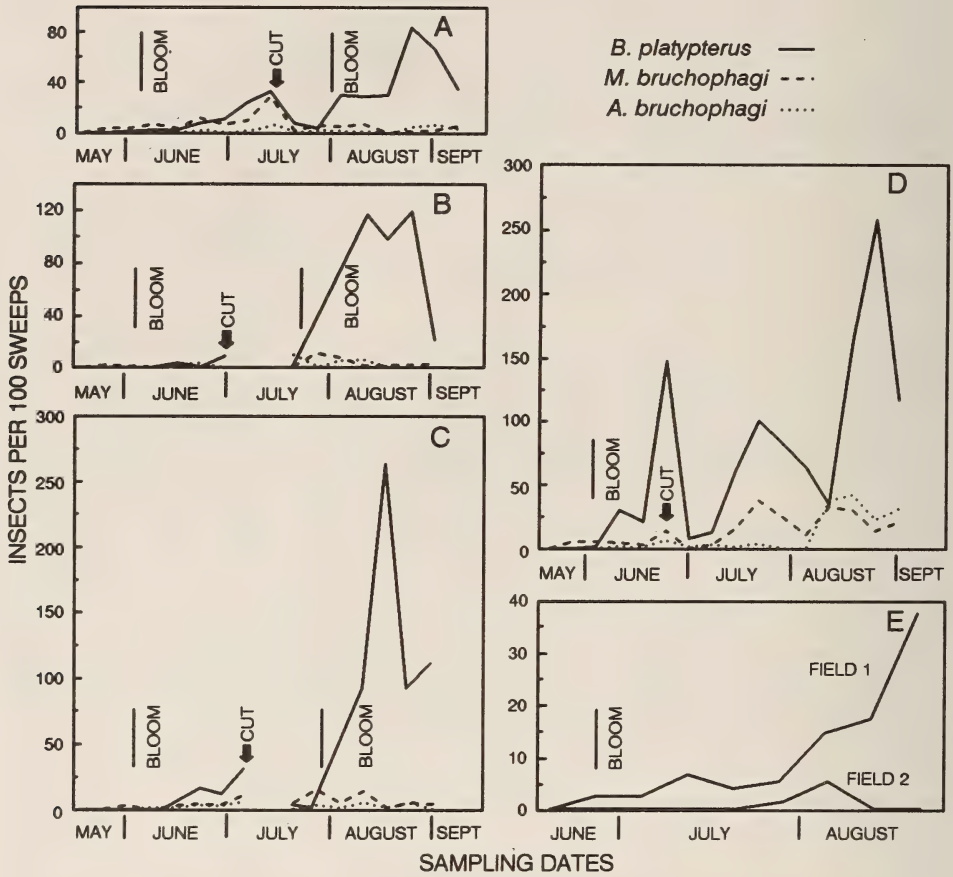

FIGURE 1. Numbers of *B. platypterus* and parasitoids sampled weekly in Ontario in 1989: A, B & C, fields in Haldimand-Norfolk County, southern Ontario; D, unmanaged trefoil in southern Ontario; E, fields near New Liskeard, northern Ontario.

Number of Generations

Exit holes caused by chalcids were found in some mature pods in August in both southern and northern Ontario, confirming that a partial second generation occurs throughout the province. The earliest part of the population in southern Ontario fields is destroyed in the hay crop, and oviposition in the regrowth seed crop is late enough that most of the chalcids enter diapause. Because unmanaged trefoil is not cut, chalcids develop earlier, and this trefoil contributes more adults for the second generation than do the seed fields. Some of these adults undoubtedly disperse to regrowth seed fields where some new pods are still developing that provide oviposition

sites. Thus, second-generation chalcids from unmanaged trefoil are important in the regrowth seed fields of southern Ontario.

Seasonal Level of Infestation in the Field

In southern Ontario, higher levels of infestation were noted on wild trefoil than in commercial fields. About 20 to 50% of the seeds dissected after July were infested (Table II). Because the first crop was cut for hay, pods only became available in the commercial fields for sampling in mid-August. The level of infestation in the commercial fields ranged from about 3 to 44%. Infestation was somewhat higher in the earliest-set seeds but dropped later in the season when the number of seed pods increased. Similar trends of infestation were reported on trefoil in California (Batiste 1967) and on alfalfa in the southern Great Plains (Ahring *et al.* 1984). In both cases, the decline in infestation later in the season was due to the large number of pods relative to the chalcid population.

Levels of infestation in the field rose to over 50% at times and exceeded the levels found in samples of dry seeds at the end of the season (Table II). Estimating chalcid infestation using samples of harvested and screened seed probably underrates the problem as some infested seeds, being lighter in weight, are lost during handling.

Effect of Pre-bloom Sprays on *B. platypterus*

A pre-bloom dimethoate spray did not reduce the percentage of chalcid-infested seeds either on the first cut or the regrowth seed crop (ANOVA; $F = 0.57$; df = 1,96; $P = 0.45$) (Table III). Actually, very few chalcids had emerged from overwintered seeds to be targets of the spray applied on the first cut on 1 June 1989. Although there were more chalcids in the fields when the regrowth crop was sprayed on 2 August 1989, a paired-comparison t-test on the population of chalcids pre-spray and two days post-spray showed no significant decrease ($t = 0.85$; df = 15; $P = 0.40$), and by five days post-treatment populations in the plots increased to about 60 chalcids/ 100 sweeps. The increase in chalcid numbers was partly because of continued emergence, and partly a result of immigration from the non-sprayed areas of the field. These results with dimethoate agree with those of Peterson *et al.* (1992b) who found that malathion was ineffective for chalcid control in Wisconsin. Even if there were insecticides effective against seed chalcids, applying them before bloom to avoid killing pollinators would not coincide with highest populations of chalcids in the field.

Field-to-field variation in the percent of infested seeds ranged from 3 to 45% ($F = 98.05$; df = 3,96; $P = 0.0001$) (Table III). The data also show a five-fold increase in infestation from about 3.8% of seeds from the first cut as compared with 19.1% on the regrowth seed crop ($F = 279.79$; df = 1,96; $P = 0.0001$). This difference indicated that producing seed from the first cut would reduce chalcid problems. However, growers prefer to take a hay crop first and then the seeds from the regrowth because the amount of plant material to process for seeds is greatly reduced.

Cultural Practices Related to Infestation of *B. platypterus*

Bruchophagus platypterus emerged from 9 out of the 10 samples of screenings collected from a compost dump in southern Ontario. Therefore seed cleaners may cause more serious chalcid problems in nearby seed fields. Antonova and Bazyleva (1964) found that infested seeds were concentrated more in screenings than in cleaned alfalfa seeds. Effective disposal of screenings by burning or burying them is an important management tactic to help reduce chalcid problems.

TABLE II. Infestation by *B. platypterus* in trefoil seeds dissected from newly matured (light brown) umbels collected throughout the season and from seed samples at harvest from three commercial fields and unmanaged trefoil in Haldimand-Norfolk County, Ontario, 1989.

Field Date	Sample size		Infested seeds	
	Umbels	Dissected seeds	Number	%
Field I:				
26 August	9	430	103	24.0
2 September	12	414	43	13.7
7 September	20	928	68	7.3
Post-harvest		700	184	26.2±2.8
Field II:				
18 August	14	475	149	31.4
26 August	19	946	68	7.2
2 September	20	800	29	3.6
Post-harvest		700	49	7.0±0.7
Field III:				
26 August	6	167	59	35.3
2 September	19	657	287	43.7
Post-harvest		700	61	8.7±1.3
Unmanaged trefoil:				
14 July	6	194	85	43.8
21 July	8	556	18	3.2
28 July	14	509	145	28.5
5 August	19	872	166	19.0
11 August	20	500	262	52.4
18 August	15	280	93	33.2
26 August	4	89	18	20.2
2 September	10	136	55	40.4
Post-harvest		700	102	14.6±2.9

In June, adult chalcids were more numerous in old fields, and progressively decreased with increasing distance into adjacent new seed fields ($F = 5.99$; df = 4,11; $P = 0.008$) (Fig. 2A and B). A similar trend was observed in August ($F = 9.58$; df = 4,11; $P = 0.001$), but there were fewer chalcids in the old fields (Fig. 2C and D). The lower populations in the old fields in August could have resulted from dispersal of chalcids to more attractive sites. When seeds were harvested, the highest level of infestation occurred in seeds collected closest to the old fields ($F = 29$; df = 3,51; $P = 0.0001$) (Table IV). Antonova and Bazyleva (1974) reported that alfalfa growing in the vicinity of old fields in the USSR tended to be severely infested by seed chalcids. Under favourable conditions the alfalfa seed chalcid can disperse 1250 m in six days (Strong *et al.* 1963). Therefore old fields should be well separated from new fields to minimize the spread of seed chalcids. Because chalcids were also more numerous on unmanaged trefoil, seed fields should also be well separated from unmanaged trefoil pastures and trefoil along roads and in wastelands.

TABLE III. Comparison of infestations by *B. platypterus* on first cut versus second cut, and on sprayed versus non-sprayed plots at four fields in Haldimand-Norfolk County, Ontario, 1989.

	Sample size	Mean percentage of infested seeds	
		First cut	Second cut
Fields			
1	14	3.0±0.8	7.7±1.3
2	14	4.9±0.8	18.6±2.3
3	14	8.9±1.0	5.3±1.2
4	14	3.5±0.9	44.8±3.8
Plots			
Sprayed	28	3.6±1.6	20.0±2.1
Control	28	3.9±0.7	18.3±2.1
Overall[1]	56	3.8±1.2 b	19.1±2.1 a

[1] Means in row followed by same letter are not significantly different using Duncan's multiple range test ($P = 0.05$).

TABLE IV. Levels of chalcid infestation in trefoil seed collected from old fields and from various locations of adjoining new fields in Haldimand-Norfolk County, Ontario, 1989.

Distance from old field (m)	Sample size[3] (n)	% Infested seeds[1] (Mean ± S.E.)
50	14	34.7±2.9 a
100	14	27.2±2.9 b
150	14	17.2±1.3 c
0[2]	14	12.1±1.4 c

[1] Means followed by the same letter are not significantly different using Duncan's multiple range test ($P = 0.05$)

[2] Represents the old field.

[3] n represents 14 samples of 100 seeds each.

Acknowledgments

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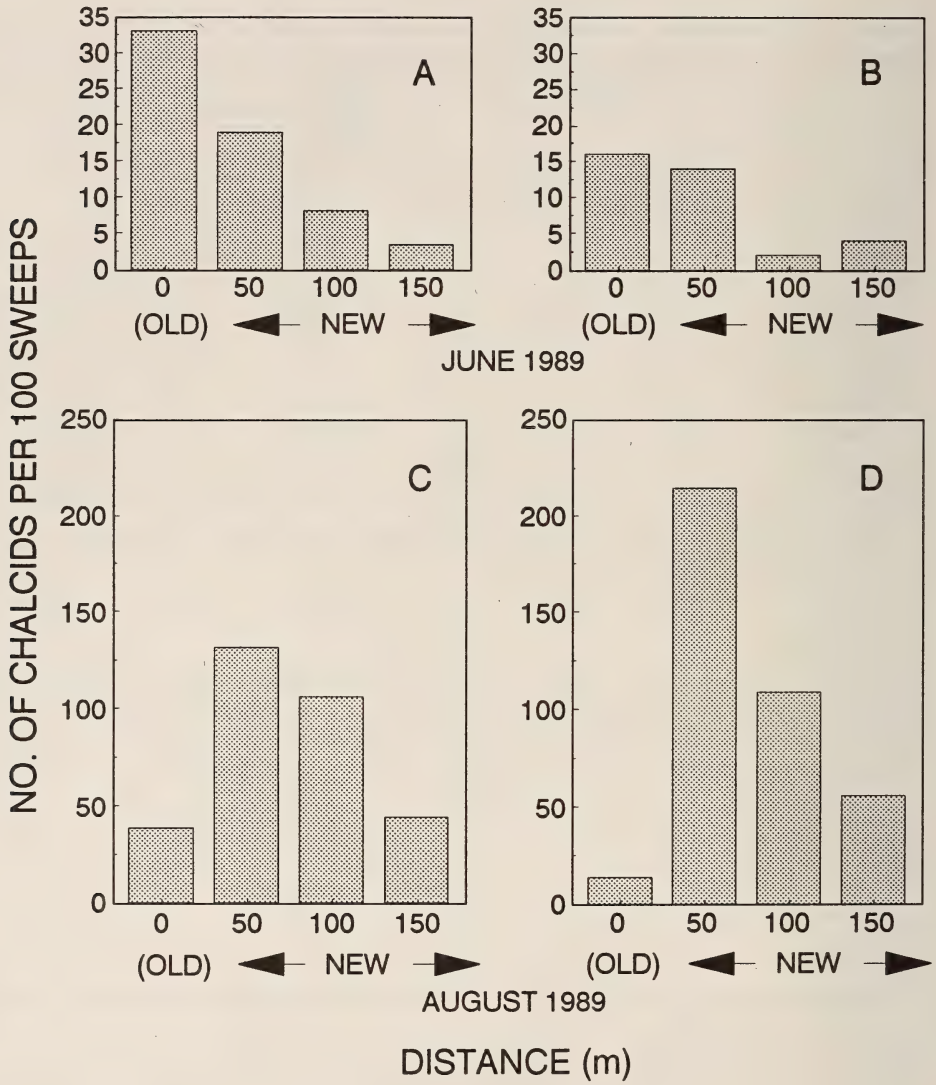

FIGURE 2. Number of adult seed chalcids in old fields and at 50, 100 and 150 m distances into adjacent new fields in Haldimand-Norfolk County, Ontario: A & B, two locations in June, 1989; C & D, same two locations in August, 1989.

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HESSIAN FLY (DIPTERA: CECIDOMYIIDAE): BIOLOGY IN SOUTHERN ONTARIO AND MASS REARING USING CONTROLLED ENVIRONMENT ROOMS

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Abstract *Proc. ent. Soc. Ont.* 123:123-131

A mass rearing technique for Hessian fly, *Mayetiola destructor* (Say) by using controlled environments enabled production of >900 puparia per flat and overall survival of 73.7 and 84.4% for a "Western" Canada and "Ontario" biotype, respectively. Chilling of puparia in diapause was successful at 2°C for several months with no loss of vigour. Resistance tests, using five winter wheat cultivars and both biotypes, showed effective resistance to the "Western" strain only by Harus and H212-8. Hessian fly were collected either as adults or as puparia from all seven sites sampled across Southwestern Ontario. Spring wheat samples contained consistently higher infestations of Hessian fly than did winter wheat.

Introduction

Hessian fly (HF), *Mayetiola destructor* (Say), is a serious pest of wheat, *Triticum aestivum* L., in several areas in the United States (Pike *et al.* 1983; McKay and Hatchett 1984; Buntin and Raymer 1989; Kudagamage *et al.* 1990) and also occurs across Canada as a sporadic minor pest of both wheat in Western Canada and barley on Prince Edward Island (Harris 1985; Sarazin 1986). HF is regarded as rare in Ontario, probably because of generally late planting dates for winter wheat, the major wheat grown in the province and the minor importance of spring wheat which would be at an attractive developmental stage during the spring HF flight (Garland 1987). In 1990, while 5.8% of the total value of Canadian wheat was produced in Ontario, spring wheat constituted only 6% of the provincial wheat hectarage (Anonymous 1991).

Because HF also infests other species of grasses such as *Agropyron* spp. (wheat grasses) and *Elymus* spp. (wild rye) (Pike and Antonelli 1981), exports of hay products from Canada have been closely scrutinized to prevent the introduction of HF into HF-free countries. This export restriction prompted hay producers and trade officials to request development of fumigation protocols for baled hay which would ensure export of HF-free product. Because no HF cultures were established in Canada, the London Research Centre was approached to provide large numbers of diapausing insects for protocol evaluation.

HF were thus collected and two populations established:

1) "Western" biotype collected during 1987 from wheat stubble in Alberta and Manitoba.
2) "Ontario" biotype collected during 1989 from winter wheat on the London Research Centre farm.

Both strains have been maintained since collection. Published rearing techniques, developed primarily for resistance breeding trials, utilized large areas of greenhouse space (Cartwright and LaHue 1944; McKay and Hatchett 1984). Lack of exacting environmental control limited rearing

to fall and winter periods when greenhouse temperatures could be controlled within the narrow limits necessary for continuous HF production. As such techniques were not suitable for year-round production of the large HF numbers required, we proceeded to develop the following rearing procedure for laboratory production.

In addition, in view of a pronounced lack of field data on HF biology, particularly for Eastern Canada, we collected data on HF populations at various locations in Southern Ontario and compared susceptibilities of five winter wheat cultivars to both HF strains.

Methods

Mass Rearing

Wheat (cv. Augusta) for rearing, was planted in standard (53 x 28 x 6 cm deep) plastic flats containing 4 cm of sandy loam potting soil. Twelve evenly spaced rows were seeded producing an average of 225 plants/flat. All flats were germinated in a greenhouse programmed for 16 h L at 25°C: 8 h D at 20°C, with supplementary lighting during the fall and winter months.

Under these conditions, wheat reached the two leaf stage within 7 days. A portable cage, consisting of fine-mesh fabric sleeve supported by a wire hoop frame ca. 30 cm high and sized to fit the periphery, was then placed over each flat. A total of 25-30 pairs of newly eclosed HF, collected early in the photophase to ensure a high rate of oviposition, were then released in each cage.

All cages were transferred to a cart situated in the centre of an insectary maintained at 20±1°C, 70±5% RH, and 14:10 L:D. Lighting, supplied by 72 F72T12 CWHO Sylvania® fluorescent tubes vertically mounted around the walls of the room, produced up to 2000 ft.-candles of light 30 cm from the wall at a point 1 m above the floor. Sleeves were removed from each flat after 48 h. Flats were then held on shelves, three tiers high, which lined the perimeter of the room. All flats were watered daily with a dilute fertilizer solution consisting of 10 g of 20-20-20 fertilizer in 6.5 L of water. During HF larval development, outbreaks of downy mildew on wheat plants were prevented by weekly misting with an elemental sulfur solution at 5 g/L of water.

Flats were harvested on completion of pupariation, within 21 days of oviposition. Roots and leaves were trimmed and all loose soil remaining on stems was removed by gentle shaking. To satisfy diapause requirements, harvested stems were wrapped in moist paper towel and placed in a plastic-wrapped box (50 x 35 x 10 cm) maintained at 2.0±1°C, 0:24 L:D for at least 10 weeks (Harris and Rose 1989).

HF required to maintain cultures were harvested as above, and placed directly into cylindrical acetate cages (41 cm H x 36 cm diam.) for eclosion at rearing conditions described above. These stems were covered with paper towel and misted regularly to promote maximum eclosion. To estimate rates of HF infestation/flat and numbers of puparia/stem, two flats per week were examined by sampling 50 wheat stems per flat for HF puparia.

Comparative Susceptibility of Winter Wheat to HF Biotypes

Five cultivars of winter wheat (Annette, Ena, Augusta, Harus, H212-8) were exposed to both the "Western" and "Ontario" HF biotypes. Wheat was planted for testing in standard (53 x 28 x 6 cm deep) plastic flats containing 4 cm of sandy loam potting soil. Two rows of each wheat variety were planted 2.5 cm apart across the flat (ca. 20 seeds/row). A 5 cm wide buffer zone separated each cultivar. Seeds were covered with 1.0 cm soil, watered and placed in a greenhouse operating at conditions described above in the section of Mass Rearing.

Plant growth regimes and insect cage design were similar to the mass rearing protocol described earlier. Approximately 45 pairs of newly eclosed HF from the rearing stock were added to each test cage, after which all cages were transferred to the insectary. Cage covers were removed after 48 h and all leaves checked for the presence of HF eggs. Experiments testing the "Western" biotype were repeated three times while the "Ontario" biotype was evaluated twice at a later date. Flats were harvested 22 to 24 days after oviposition and all stems checked for presence of puparia.

Field Biology in Southern Ontario

a) Adult Phenology

During 1988, HF were monitored near St. Thomas (1) and Bryanston (2) (Fig. 1), using 11 x 22 cm yellow cardboard sticky traps, stapled, 65 cm above the ground, to wooden stakes. A total of 5 traps, 15 m apart, were established at each location and were changed weekly until the end of October. At the St. Thomas location, traps were established 19 April along the border of a wheat field and a grassed waterway. At Bryanston, traps were established 26 April along the edge of a wheat field and a municipal drain. To identify HF, traps were returned to the laboratory and scanned using a binocular microscope.

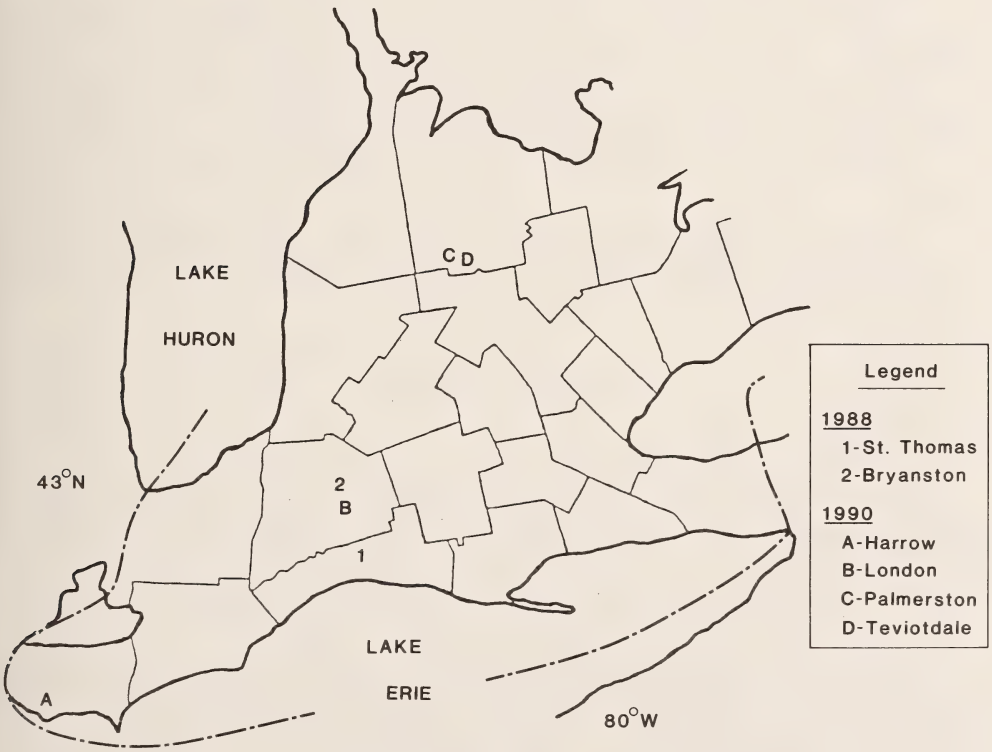

FIGURE 1. Location of sampling sites of *Mayetiola destructor*.

A pheromone trap was designed to attract male HF during 1990. One-week-old wheat seedlings in 10 cm plastic pots were covered with a cheesecloth cover supported by three 15 cm wooden stakes. Five to ten newly eclosed female HF, whose protruding ovipositors evidenced pheromone emission (McKay and Hatchett 1984), were aspirated into each of four cages. HF were monitored from 08:00-09:00 hours in a wheat plot planted the previous fall on the London Research Centre farm. Cages were placed 5 m apart in the plot. Over the course of one hour, each cage was observed closely, in rotation, for 5 minutes before moving to the next cage; each cage was thus observed for a total of 15 minutes during the observation period. Sampling began 01 May 1990 and continued twice weekly until the end of HF flight activity. HF attracted to the cages were collected by aspiration. Sampling began again 04 September 1990 and continued until no further HF were collected.

b) Field Infestation

HF infestations were monitored at four locations (Fig. 1): Agriculture Canada Harrow Research Station (A), London Research Centre (B), Palmerston (C), and Teviotdale (D). Experimental and registered cultivars of both fall and spring wheat were planted at A and C while larger plantings of registered varieties were established at B and D. Because many samples were from small plot variety trials, numbers of stems that could be taken were limited.

Spring wheat was sampled by randomly removing from each replicate all plants, including roots, from 30 cm of row. The total number of plants, the rate of infestation, and the number of HF per plant were recorded. Winter wheat was sampled by removing groups of 50 stems at various locations across a plot or across a field (Table I) as described by Foster and Taylor (1975). All samples were individually bagged, returned to the laboratory, and held at 1±1°C. Each sample was checked for presence of HF puparia at the nodes of winter wheat stems and in all tillers of spring wheat. Numbers of infested stems or plants and numbers of puparia/stem or/plant were recorded.

Text observations are presented as means ± S.E.M. Data were subjected to analysis of variance using MSTAT-C; where necessary, means were separated (P=0.05; 0.01) using an LSD test (MSTAT Development Team 1988).

Results and Discussion

Mass Rearing

Environmental conditions in our experiments were similar to optimum rearing temperatures published by Foster and Taylor (1975). High light intensity and regular fertilization produced robust wheat seedlings suitable for HF development. Each insectary held 75 production flats at any one time because with the high light intensity from the vertical lighting, three levels of shelving could be utilized. Placing oviposition cages in the centre of the insectary for the initial 48 h reduced positive HF phototactic response and resulted in even distribution of eggs throughout rearing cages.

The mass rearing technique described permitted year round production of ca. 20 HF-infested flats per week for use in various experiments. Two flats were sampled for quality control assessment and subsequently used for further insect production while the remainder were kept in cold storage for induction of diapause. Overall productivity averaged approximately 900 HF puparia per flat as determined by the quality checks of 50 stalks/flat. Infestation levels for the "Western" biotype averaged 75.0±3.4% per flat and 5.1±0.3 puparia/stalk.

TABLE I. Field infestations of *Mayetiola destructor* on Ontario wheat, at various locations during 1990.

Cultivar	Preceding crop	n	Mean # plants-stems/sample	Mean # pupae/sample	Mean % plants-stems infest/sample
		Spring Wheat			
Harrow	sampled June 26				
Fielder	winter wheat	3	14.6	18.3	54.5
SWS-89	winter wheat	3	20.0	18.6	41.6
SWS-59	winter wheat	3	15.6	35.3	74.5
SWS-67	winter wheat	3	12.0	31.7	69.4
SWS-87	winter wheat	3	16.0	19.7	37.5
SWS-76	winter wheat	3	13.3	23.3	70.0
SWS-52	winter wheat	3	21.7	49.7	73.8
SWS-102	winter wheat	3	16.3	32.0	67.3
Palmerston	sampled June 20				
Celtic	canola	8	29.1	2.9	8.6
Norseman	canola	8	32.5	3.0	7.3
Katepwa	canola	8	25.8	2.6	7.7
Belvedere	canola	4	33.8	3.5	10.4
Teviotdale	sampled June 20				
Celtic	corn	15	19.1	5.3	18.5
		Winter Wheat			
London	sampled July 10				
Augusta E	clover	8	50	4.1	6.5
Augusta L	clover	8	50	1.6	2.0
Harrow	sampled June 26				
Augusta	alfalfa	4	50	3.3	4.5
Harus	oats	4	50	2.3	3.5
Teviotdale	sampled June 20				
Absolvent	soy beans	15	50	3.2	0.7

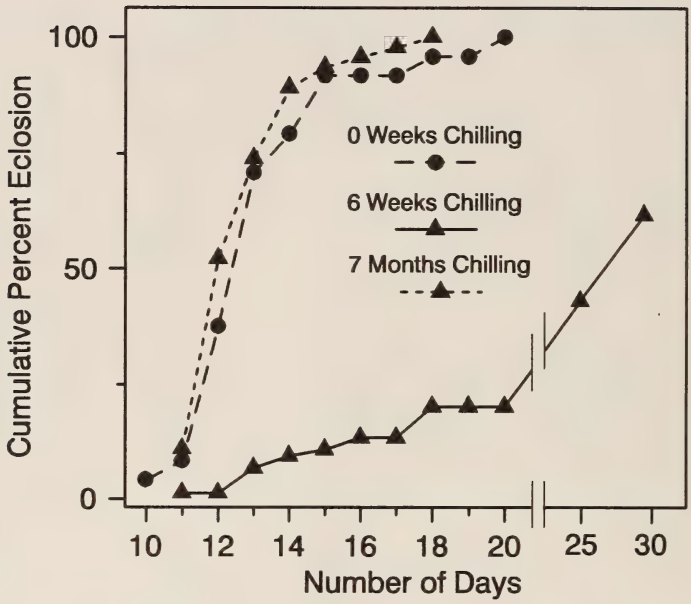

FIGURE 2. Eclosion of laboratory-reared "Western" biotype of *Mayetiola destructor* at 20°C.

Life history parameters were determined using both the "Western" and "Ontario" biotypes. Average egg production was 153.8±13.34 eggs/female with 83.7±4.4% hatch for the "Western" biotype and 132.7±23.5 eggs/female with 85.8±3.9% egg hatch for the "Ontario" biotype. Further calculations determined overall percent survival of 73.7±7.0 and 84.4±4.1 for "Western" and "Ontario" biotypes respectively.

Diapause was induced by placing the harvested puparia into cold storage at 1-2°C for at least 10 weeks (Harris and Rose 1989). If at least 75% relative humidity were maintained throughout the pupal development period, pupal survival (95% +) and number of days to 50% eclosion (12±.5 d) were similar for HF either taken directly from rearing flats or chilled for seven months. Removal of puparia from cold storage before the end of diapause fulfilment caused reduced and delayed emergence of adults (Fig. 2), a phenomenon that occurs in other Dipterans as well (Tolman *et al.* 1985).

Comparative Susceptibility of Winter Wheat to HF Biotypes

Highly significant ($P<0.01$) differences in susceptibilities to the "Western" HF biotype were observed among the 5 tested winter wheat cultivars; both Harus and H212-8 were effectively resistant (Table II). The parental cross for Harus was Fredrick x Yorkstar, and H212-8 was derived from a Harus x Augusta cross.

Although no effective resistance was evident for any cultivar exposed to the "Ontario" HF biotype (Table II), infestation rate of H212-8 was significantly lower ($P<0.05$) than in other

cultivars. The lack of resistance to the "Ontario" biotype may be the result of adaptation by local HF populations, over generations of exposure, to wheat cultivars having the same genes for resistance. Similar adaptations have been documented in several areas of the United States spurring research to discover more genes for resistance and the development of strategies to maintain resistance of currently available cultivars (Cox and Hatchett 1986; Ratanatham and Gallun 1986; Kudagamage *et al.* 1990).

TABLE II. Comparative susceptibility of winter wheat cultivars to "Western" and "Ontario" biotypes of *Mayetiola destructor*.

Wheat cultivar	Western biotype (n=3)			Ontario biotype (n=2)		
	Mean # plants	Mean # infest[1]	Mean % infest	Mean # plants	Mean # infest[1]	Mean % infest
Ena	41.3	41.3 a	100.0	35	32.5 a	92.9
Augusta	41	40.3 ab	98.3	35	34 a	97.1
Annette	41.3	39.3 b	95.2	35	34 a	97.1
Harus	42	2.0 c	4.8	35	33 a	94.3
H212-8	39	0.0 d	0.0	35	30 b	85.7

[1] Within each column, means followed by the same letter are not significantly different (P=0.05) as determined by an LSD test.

Field Biology in Southern Ontario

a) Adult Phenology

Only 16 HF adults were tentatively identified on sticky traps; more male HF than female HF were captured. HF were captured during the periods of 04-12 May and 26 May - 02 June at St. Thomas and HF were collected at Bryanston only during the week of 12-19 May. No HF were identified during the rest of the growing season.

Because of the low success of sticky boards for HF monitoring, the potential of pheromone attraction was evaluated in 1990. McKay and Hatchett (1984) demonstrated attraction of both virgin and mated male HF to virgin female HF. Several newly eclosed, pheromone-emitting female HF confined in a loose-weave cheesecloth cage with a pot of wheat seedlings as resting sites, produced a simple pheromone attractant. We did not attempt to estimate range of attractiveness, using the device only to determine presence of male HF on a given date. The spring HF flight began 09-14 May and continued until 01 June 1990. The fall flight period began 10-13 September and continued until 02 October 1990. In 1990, winter wheat planted by growers relying on the published "fly free" dates of 07-15 September for Zone 3 in southern Ontario (Garland 1987) would have been exposed to ovipositing HF. However, southern Ontario winter wheat is sown mostly during October, and seedlings emerge after the main HF flight period.

b) Field Infestation

After determining that none of the tested winter wheat cultivars showed effective resistance to the "Ontario" HF biotype, a number of wheat fields around southern Ontario were checked for HF. Puparia were found in all checked cultivars at all locations (Table I). Significantly more ($P<0.05$) puparia were found on an early planting of Augusta wheat at London than on a late planting. We surmise that this resulted from a higher overwintering HF population on the early planting. Although numbers of HF were higher on spring wheat than on winter wheat at both Harrow and Teviotdale (Table I), it is likely that these infestation differences are the result of differences in plant attractiveness during the HF flight rather than to genetically determined differences in cultivar susceptibility to HF. Buntin and Raymer (1989) showed that susceptible winter wheat incurred the highest infestations during the seedling stage, which would correspond to the early planted winter wheat at London and the various spring wheat plantings at the other locations. Numbers of insects per 30 cm row of spring wheat were generally lower in all Ontario locations that we sampled, compared to those in the susceptible winter wheat varieties as determined by Buntin and Raymer (1989).

Numbers of puparia collected and percent plants infested were consistently higher in the spring wheat cultivars (Table I). It is not clear whether infestations of the level that we found would have affected crop yields. Buntin and Raymer (1989) concluded that forage yields from winter wheat did not decline until infestations of tillers exceeded 10% and that numbers of tillers/plant did not decrease until infestation levels reached 50% or greater. We surmise that, with infestation levels ranging from 37.5 to 74.5%, some yield reduction would have occurred in the Harrow spring wheat plots (Table I). The observation that highest HF infestations, in Harrow spring wheat, were recorded in plots seeded with wheat the previous year, emphasizes the benefits of crop rotation, particularly if HF-susceptible spring wheat is grown.

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YELLOW PAN WATER TRAPS FOR MONITORING THE SQUASH VINE BORER, *MELITTIA CUCURBITAE* (LEPIDOPTERA: SESIIDAE) IN HOME GARDENS

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London ON N6G 2V4 Canada

Squash vine borers, *Melittia cucurbitae* (Harris) are persistent, but sporadic pests in home gardens throughout eastern and mid-western North America that can also cause losses in commercial plantings of various Curcubitaceae (Whitcomb and Garland 1948; Mackay 1968). In Ontario, commercial plantings of squash, melons and pumpkins are routinely treated with 4 weekly applications of pesticide aimed at ovipositing adults beginning at the end of June (Anonymous 1992). Anecdotal accounts indicate that squash vine borers can cause losses in home gardens and some gardeners have given up growing squash and pumpkins because of it. During the first year of an investigation on the control of root maggots in home gardens with *Aleochara bilineata* (Gyllenhal) (Coleoptera: Staphylinidae) (Tomlin *et al.* (1992)), we discovered that squash vine borers were captured by Yellow Pan Water Traps (YPT) used to monitor adult cabbage maggot, *Delia radicum* (L.) and onion maggot, *D. antiqua* (Meigen) (Diptera: Anthomyiidae). YPT were first used (Moericke 1950) to monitor populations of aphids and were subsequently used by many researchers to monitor *Delia* spp. and other insects (Southwood 1978). We present in this note collection records from YPT for squash vine borers monitored for three years in home gardens in London, Ontario, Canada.

In 1988, pans used in these tests were stainless steel salad bowls 15 cm in diameter by 5 cm deep painted, on the inner surface, with Tremclad® yellow paint (Tremco, Ltd., Toronto, Ontario). In 1989 and 1990, similar sized yellow plastic bowls (Design Motivation Ltd., Toronto, Ontario) were used. Pans were filled with saturated $CaCl_2$ solution with a few added drops of Kodak Photo-Flo 200® to reduce surface tension and a few grains of sodium benzoate to prevent fungal/ microbial degradation of captured specimens. The YPTs were placed in the centre of 1 m x 4-5 m experimental plots of onions and radish in gardens that ranged in size from 45 - 200 m^2. Captured specimens were removed from the traps weekly from May to September. We sampled 28, 29 and 28 gardens in 1988, 1989 and 1990 respectively. All gardens had various species of cucurbits growing through the season. Values in Figure 1 are the total number of squash vine borers captured per week in all gardens from June to September.

Degree days were calculated from 1 March by the method of Baskerville and Emin (1969) using maximum and minimum temperature values for London, Ontario provided by Environment Canada.

There were 3.46±2.68 (mean ± S.D.) squash vine borers per garden per year over all years with only one garden out of 20 monitored for 3 consecutive years in which no moths were captured. The highest number of individuals captured per garden per year was twelve. There was a single generation of squash vine borer per year in London (Fig. 1); the flight period began at the end of June and peaked from July 10 (1988) to July 24 (1990).

When degree days to 50% emergence were calculated for the three years over a range of base temperatures from 5 to 15°C, and the coefficient of variation analyzed (Litsinger and Apple 1973) it was found that a base temperature of 11°C best fit the data. Based on these findings, first emergence can be expected at around 354 $DD_{(11)}$±31 (mean ± S.D.).

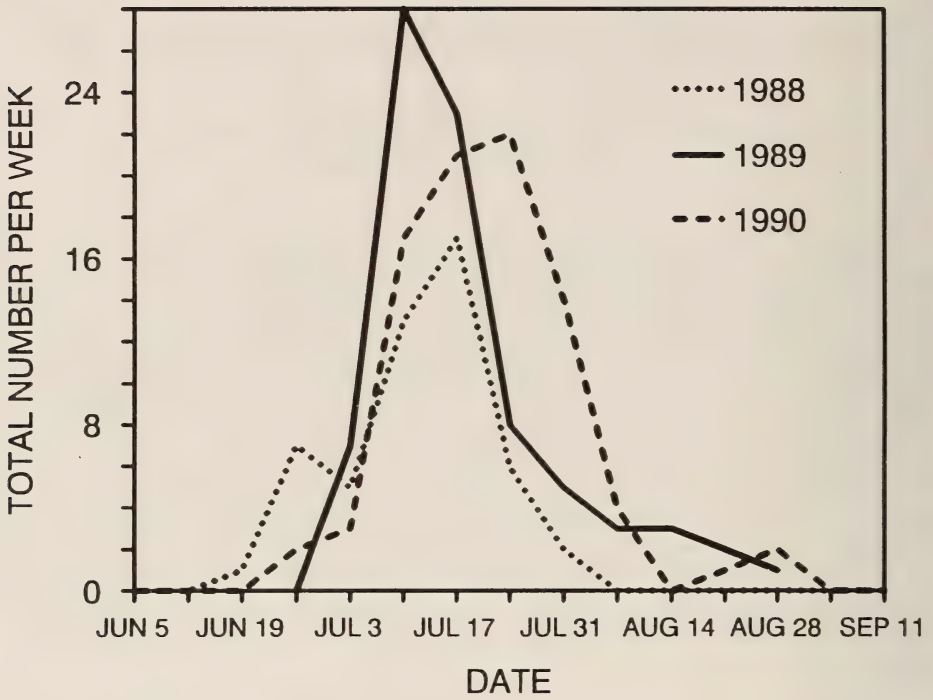

FIGURE 1. Total weekly captures of squash vine borer, *Melittia cucurbitae*, in yellow pan water traps in home gardens in 1988, 1989 and 1990 in London, Ontario.

In 1989 and 1990, bowl traps painted on the inner surface with Tremclad® white paint and placed in 7 gardens each year caught only one squash vine borer moth during that time (mean ± S.D. = 0.07±0.26 moths per trap per year) while YPT in 21 gardens during the same years caught 169 moths (mean ± S.D. = 4.02±2.7 moths per trap per year). Apparently the yellow colour was more attractive to the squash vine borer than the white ($t_{.05\,[54]} = 5.343$, $P < 0.001$).

Although we do not know if captured squash vine borers reduced populations sufficiently to affect the number of damaged squash vines and fruit in home gardens, YPT traps can indicate the presence of squash vine borer so that appropriate control measures could be applied. The reddish coloured moths can be identified easily by home gardeners. These traps may also prove of value as a monitoring tool for squash vine borer in commercial plantings of Cucurbitaceae.

Acknowledgements

We thank G. Steele, D. Ferris, R. Knight and J. Mitton for their technical support. We appreciate the cooperation and encouragement of the London Horticultural Society and K. Smith of the London Free Press. Partial financial support was provided by the Ontario Ministry of the Environment through the Ontario Pesticides Advisory Committee.

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(Received 23 October 1992; Accepted 9 December 1992)

THE ENTOMOLOGICAL SOCIETY OF ONTARIO
CONSTITUTION AND BY-LAWS

Historical Profile

The Entomological Society of Ontario was incorporated on the 15th of February, 1871, by Section 9 of Chapter 23 of Statutes of Ontario, 1871, (34 Vic., Cap. 23) being an Act to amend The Agricultural and Arts Act as follows:

The following section from the Act described the purpose of the Society:

> "The Society now existing known as the "Entomological Society of Canada", may organize and form themselves into a society, comprising not less than twenty five members, and paying an annual subscription of not less than one dollar each, to be known as "The Entomological Society of Ontario", and shall have power to adopt a constitution, and make by-laws for the admission of members, and for its guidance and proper management and the promotion of any objects consistent with the study of Entomology, and its practice bearing upon the agricultural and horticultural interests of the Province; and on filing a copy of such constitution and by-laws with the Commissioner of Agriculture such society shall become a body corporate under this Act.
>
> The society was empowered to amend its constitution following procedures specified within its constitution, and to make, repeal or amend by-laws under the terms of said constitution. Amendments or by-laws became effective upon the date specified, upon filing a copy with the Commissioner of Agriculture.

CONSTITUTION

Name — ARTICLE 1

(1) The corporation shall be known as the Entomological Society of Ontario, herein after the Society.

(2) The headquarters and library of the Society shall be situated at the Ontario Agricultural College of the University of Guelph.

(3) The seal of the Society bears two concentric circles, the inner enclosing a line drawing of a monarch butterfly superimposed on an outline map of Ontario; the outer ring contains the inscription in Old English Type.

Entomological Society of Ontario 1863

Objects — ARTICLE 2

The objects of the Society shall be to serve as an association of persons interested in the study of insects and to promote the science of entomology in all its aspects, with special emphasis upon the interests of the Province of Ontario.

Membership — ARTICLE 3

(1) Membership is open to any person interested in entomology upon payment of the prescribed dues.

(2) The classes and conditions of membership and appropriate dues for each class shall be established by By-Law.

Fellows ARTICLE 4 A Member or former Member who has made an outstanding contribution to the advancement of entomology shall be eligible for election as a Fellow of the Society, the mode of election being determined by By-Law.

Governing Board ARTICLE 5 The general management of the Society shall be vested in a Governing Board consisting of the Directors and the Officers: President, Past-President, Vice-President (President-Elect), Secretary, Treasurer or Secretary-Treasurer, and Editor. The number of Directors, their mode of election, and the mode of election of the Officers shall be determined by By-Law.

Meetings ARTICLE 6 (1) The Society shall hold an Annual Meeting at such time and place as may be determined by By-Law.

(2) At each Annual Meeting, the Governing Board shall present a full report of their proceedings, and of the proceedings of the Society, and a detailed statement of the receipts and expenditure for the previous year, and of the assets and liabilities, duly audited.

(3) Other meetings may be called under the conditions established by By-Law.

Election of Auditors ARTICLE 7 (1) The Board of Directors at the time of the Annual Meeting shall select an auditor or auditors to audit the accounts of the Society, to hold office until the next Annual Meeting.

(2) The fiscal period of the Society shall be the calendar year.

Amendment ARTICLE 8 (1) Proposals to amend or repeal the Constitution of the Society shall be made by the Governing Board or by ten Members in good standing in a signed letter to the Secretary, and shall be transmitted to the Members with the notice of the next following Annual Meeting.

(2) The constitution may be amended or repealed by a two-thirds majority vote of Members, the vote being taken subsequent to a discussion at an Annual Meeting, by a letter ballot distributed not later than the ballot for the next annual election.

Amendments of the By-Laws ARTICLE 9 (1) Proposals to amend the By-Laws may originate from or be presented to the Governing Board, and shall be transmitted to the Members with the notice of the next following Annual Meeting.

(2) By-Laws may be amended by a majority vote of Members at the Annual Meeting, or by mail ballot as decided by the Governing Board.

BY-LAWS

Membership By-Law 1

(1) The Society have the following classes of membership:

(a) regular membership, consisting of those persons interested in entomology, who have paid the prescribed dues and are entitled to all the privileges of the Society, including a single vote in any general ballot of the membership, election to an office of the Society, and a copy of the annual report of the proceedings of the Society.

(b) honourary membership, consisting of Members of the Society who, upon retirement, wish to continue with all rights and privileges of the Society, other than voting; there are no dues.

(c) sustaining membership, consisting of those corporations, companies and like bodies that are interested in promoting the objectives of the Society and have paid the prescribed dues. Rights and privileges are those of a single regular Member.

(d) fellows, consisting of those persons accepted as Fellows of the Society through elective procedures outlined elsewhere in these By-Laws. Rights and privileges are as for Regular Members; there are no dues.

(e) student membership, consisting of Members who are currently registered as students at an academic institution.

(f) amateur membership, consisting of persons who have an amateur interest in entomology.

(2) Acceptance into membership in any class shall be subject to the approval of the Governing Board.

(3)

(a) Dues for the different classes of membership shall be determined from time to time by resolution of the Governing Board and fixed and approved by By-Laws passed at an Annual Meeting.

(b) Membership dues shall be payable to the Treasurer January 1st for the current year.

(4) A Member may resign from the Society by delivering a written resignation to the Secretary, but upon resigning shall not receive any refund of dues.

(5) A Member who has not paid the membership dues in full by the last day of the fiscal year shall, upon due mailed notice at the last known mailing address, cease to be a member, but he/she may be reinstated upon payment of unpaid dues in full, and where a person who ceased to be a member of the Society for failure to pay dues in full re-applies for membership, he/she shall submit payment of all dues payable during the year prior to the re-application for membership as well as dues for the current year.

Annual and Special — By-Law 2

(1) The time and place of the Annual Meeting shall be General Meetings determined by By-Law passed at an Annual Meeting. Such an Annual Meeting shall normally be held in September, October, November or December.

(2) A special meeting of the Society may be called by the Governing Board or at the written request of fifteen Members of the Society, and shall be held at the headquarters of the Society.

(3) Notice in writing of the time and place of the Annual Meeting or a special meeting shall be mailed by the Secretary to the Members not less than fourteen days in advance of the holding of such meetings.

(4) The Secretary shall include in any notice respecting a special meeting a statement of the business to be transacted and no other business shall be transacted at such meeting.

(5) A Member may vote by proxy at a special meeting provided that in a signed statement delivered to the Secretary in advance of the meeting he name a proxy who is a Member of the Society in good standing.

(6) An Annual or special Meeting , on a majority vote, may be closed to all persons not Members of the Society.

(7) 15 Members of the Society shall form a quorum at an Annual Meeting or at a special meeting.

Officers — By-Law 3

(1) The Officers of the Society shall be the President, Past-President, Vice-President, Secretary, Treasurer or Secretary-Treasurer, and the Editor.

(2) (a) The President, Past-President and Vice-President shall hold office for one year.

(b) The President shall be that person who has most recently completed a term of office as Vice-President. A vacancy shall be filled by the Vice-President, who will then serve his normal term as President.

(c) The Vice-President shall be that person who was most recently elected to this office. After a term as Vice-President he shall then become the President. A vacancy shall be filled by the person with the next highest number of votes in the most recent election.

(d) The Past-President shall be that person who has most recently completed a term of office as President. A vacancy shall be filled by the person who has most recently completed a term of office as Past-President.

(e) The Governing Board shall, from among themselves or otherwise, elect a Secretary and a Treasurer or a Secretary-Treasurer, an Editor and a Librarian.

Governing Board By-Law 4

(1) The Governing Board shall be comprised of six Directors and the Officers of the Society.
(2) The normal term of office of a Director shall be three years.
(3) The Governing Board shall have full power to act for and on behalf of the Society, and all grants of money and other funds of the Society shall be received and expended under their direction, subject to the By-Laws of the Society.
(4) The Board may delegate any of their powers to an Executive Committee composed of the President, Vice-President, Past-President and the Secretary and Treasurer or Secretary-Treasurer but any action taken on powers so delegated shall be recorded in minutes and shall be presented for approval by motion at a meeting of the Governing Board before the next Annual Meeting.
(5) Meetings of the Governing Board of the Society may be called by the President thereof, or in his/her absence or on neglect, by the Vice-President, or by the Past-President or Secretary in this order of authority in the absence or on the neglect of the President and Vice-President, or in the absence or on the neglect of the Officers of the Society, by any three Directors of the Society of which meeting at least seven days notice shall be given to each Officer and Director.
(6) A majority of the Officers and Directors shall form a quorum.
(7) The Directors elected at an Annual Meeting shall take office at the close of that Meeting, and at their first meeting shall elect the previous Vice-President as President, and the recently elected President-Elect as Vice-President.

Election of President-Elect and Directors By-Law 5

(1) The Members of the Society, from persons eligible for Elect and Directors regular membership, shall elect every year a President-Elect and two Directors by mail ballot, as follows:
(a) The Governing Board shall appoint a Nominating Committee comprised of a Chairman and no fewer than two other Members of the Society.
(b) The Nominating Committee shall nominate no fewer than two Members as President-Elect, and no fewer than three Members as Directors, and shall deliver these nominations, together with written acceptances by the nominees and a short biographical sketch of each nominee to the Secretary not later than the last day of December.
(c) A list of nominations made by the Nominating Committee and the accompanying biographical material shall be mailed to the Members by the Secretary not later than the last day of January.
(d) Members of the Society may nominate additional persons for Directors and for President-Elect provided that each nomination is made by no fewer than five Members and is accompanied by a written acceptance of the nomination by the nominee and is

normally delivered to the Secretary not later than the first day of May.

(e) The Secretary shall prepare and mail to the Members of the Society whose dues for the past year have been paid, not later than the fifteenth day of June, a ballot for the election of the President-Elect and the Directors that contains the names of the nominees for each office arranged in alphabetical order, and he shall provide sufficient instructions and envelopes to ensure the secrecy of the vote.

(f) The ballots shall be returned to the Secretary not later than the fifteenth day of July.

(g) The Governing Board shall appoint no fewer than two Members of the Society to act as scrutineers and to be present when the Secretary opens and closes the ballots.

(h) Each question on the ballot constitutes a separate ballot and spoiling a vote for one question does not spoil the other questions. Each question on the ballot shall be determined by a simple majority of the votes cast unless otherwise specified in the Constitution and By-Laws.

(i) The Secretary shall notify all candidates of the results of the elections.

(j) The names of the elected candidates shall be presented at the next Annual Meeting. The election of the President-Elect, and two Directors, and the appointment of the four previously-elected Directors to a second term or third term shall be formally ratified by a motion at the Annual Meeting.

By-Law 5

(2) Directors shall be eligible for re-election, but shall not hold office for more than six years consecutively.

(3) If a Director, after one year or two years in office, is elected as President-Elect, his remaining term as Director shall be filled by the losing candidate for Director having the highest number of votes.

(4) A vacancy occurring by death or resignation, or failure to qualify as a Member, of any Officer or Director may be filled by the remaining Officers and Directors of the Society, and it shall be the duty of such Officers and Directors to nominate and appoint a fit and proper person to fill the office for unexpired term of the person so dying or resigning; but, in the event of the remaining Officers and Directors being insufficient to form a quorum, or, if, for any reason, a quorum cannot be obtained, then persons to fill the vacant offices shall be elected in the manner provided in subsection 6.

(5) In the event of an election of any Directors and Officers of the Society not being held at the time and place directed by By-Law or being for any reason illegal or void, the persons in office at the time when such Directors and Officers have been elected,

shall continue to be the Governing Board of the Society until their successors are legally appointed.

(6) In the event of any such non-election or illegal election, a special meeting of the Members of the Society shall be called in the manner provided by By-Law, for the election of such Directors and Officers, and at such meeting the election of Directors and Officers shall take place, and the persons elected shall thenceforth, until their successors are appointed, be the Directors and Officers of the Society.

(7) The Society may elect as Director or President-Elect a person not a Member of the Society, but the person so elected must, within ten days, become a Member, and he shall be entitled to act as a Director or President-Elect after he has become a Member of the Society.

(8) The Society may be By-Law provide that only those Members who have paid their dues at least one week in advance of the Meeting shall be qualified to vote at the Annual Meeting for the election of Directors and President-Elect.

(9) The above procedure for election of Directors and President-Elect shall ensure that one President-Elect shall be elected from at least two candidates and that two Directors shall be elected from at least three candidates on the ballot. The President-Elect will serve for one year prior to taking office as President and each Director shall serve for a three-year term.

Representative to the Entomological Society of Canada — By-Law 6

The Governing Board shall appoint at the appropriate times a Member of the Society to act as a Director of the Entomological Society of Canada who shall normally serve as a three-year term.

Committees — By-Law 7

(1) The Governing Board shall appoint:

(a) A Library Committee comprised of a Chairman and no fewer than two other Members of the Society that shall be responsible for the orderly maintenance of the library, and the Chairman shall be the Librarian.

(b) A Publications Committee comprised of a Chairman and no fewer than two other Members of the Society that shall be responsible for all publications of the Society and shall act as an editorial board in the preparation of the annual report, and the Chairman shall be the Editor of the annual report.

(c) Such other committees as it deems necessary.

(d) Chairman of such committees appointed by the Governing Board shall be Members *ex officio* of the Governing Board.

Election of Fellows — By-Law 8

(1) Fellows are Members or former Members who have made an outstanding contribution to the advancement of entomology.

(a) Fellows shall be elected if at least two-thirds of the votes cast in a secret mail ballot are in the affirmative.
(b) A person may be nominated as a Fellow by no fewer than three members of the Society.
(c) The maximum number of Fellows of the Society shall be limited to ten at any one time and no more than two shall be elected in any one year.
(d) Nominations shall be delivered in writing to the Secretary along with a letter from the nominee indicating his/her assent.
(e) Names of nominees received by the Secretary and approved by two-thirds of the votes at a meeting of the Governing Board shall be placed on a ballot prepared by the Secretary and mailed to the Members with the next ballot for the election of Directors.
(f) The ballots shall be returned to the Secretary not later than the fifteenth day of July and shall be opened and counted at the same time and under the same scrutiny as the ballots for the election of Directors.
(g) The Secretary shall announce at the Annual Meeting the names of the persons elected as Fellows. Certificates of Fellowship in the Society shall be presented.
(h) The names of Fellows of the Society shall be published annually in the Proceedings of the Society.

Duties of Officers — By-Law 9

(1) The President shall preside at all meetings of the Society and of the Governing Board and of the Executive Committee.
(2) The Vice-President shall carry out the duties of the President in the latter's absence for any cause.
(3) The Secretary shall
  (a) record the minutes of the Annual Meeting and all meetings of the Governing Board and the Executive Committee;
  (b) maintain the list of Members of the Society;
  (c) produce a Newsletter mailed to the membership in January, May and September of each year, providing information about meetings, elections, membership activities, etc; and
  (d) perform such other duties as the Governing Board shall determine.
(4) The Treasurer shall
  (a) have charge of the funds and other assets of the Society;
  (b) make all disbursements for the Society;
  (c) receive dues and other moneys payable to the Society;
  (d) keep accurate records of receipts and expenditures; and
  (e) prepare and present to the Annual Meeting a statement of receipts and expenditures, and of the assets and liabilities, duly audited.

President's Prize By-Law 10

(1) A sum of money, the amount to be approved by the Board of Governors each year, will be given to a graduate or undergraduate student in Ontario presenting the best paper of high standard on an aspect of Entomology at each Annual Meeting of the Society.

(a) Titles of papers to be considered for the President's Prize shall be submitted on forms provided to the Chairman of the Committee responsible for the Program of the Annual Meeting by the deadline for receipt of papers for the Annual Meeting as stated by that Program Committee.

(b) The President shall, at the beginning of the Annual Meeting, select a panel of impartial judges to hear the student papers submitted for the President's Prize, and to select the paper to be named for this award.

(c) The awards(s) shall be presented at an appropriate time before the close of the Annual Meeting.

ERRATA

Broadbent, A.B. and D.W.A. Hunt. 1991. Inability of western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), to overwinter in southern Ontario. Proceedings of the Entomological Society of Ontario, 122: 47-49.

The following line of text should be inserted at the bottom of page 47 of the above paper:

nylon mesh (500 µ) and with removable plexiglass tops. On at least three occasions in August and

The editor apologizes for this omission.

1992 ANNUAL MEETING

The **Entomological Society of Ontario** is grateful for the hospitality extended by Queen's University at the **129th Annual Meeting** held in Kingston, Ontario on 23-25 October 1992.

ENTOMOLOGICAL SOCIETY OF ONTARIO

The Society, founded in 1863, is the second oldest Entomological Society in North America and among the nine oldest, existing entomological societies in the world. It serves as an association of persons interested in entomology and is dedicated to the furtherance of the science by holding meetings and publication of the **Proceedings**. The **Proceedings** publishes only fully refereed scientific papers, has a world-wide circulation, and is covered by all major abstracting and indexing services. The **Society** headquarters are at the University of Guelph. The **Society's library** is housed in the McLaughlin Library of the University and is available to all members.

An annual fee of $20 for professional entomologists, or $10 for amateurs and students, provides membership in the society, the right to publish in the **Proceedings**, and receive the **Proceedings of the Entomological Society of Ontario**.

APPLICATION FOR MEMBERSHIP

Name: _____

Address: _____

_____

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Please send cheque or money order to:
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Entomological Society of Ontario,
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NOTICE TO CONTRIBUTORS

Please refer to Volume 117 (1986), pages 103-104 for instructions to authors. Copies of those instructions are available from the Editor.

Vouchers are important. Authors are urged to deposit voucher material at recognized institutions to document their research and to cite the place(s) of deposit in their publications.

Note: Please provide figures to fit page sizes of the ***Proceedings****.*

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of the
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FRONTISPIECE. Photograph of habitus of *Coptodera brunnea*, new species, dorsal aspect. USA, Arizona, Huachuca Mtn., Ash Canyon Road (CNC). SBL = 6.16 mm.

CLASSIFICATION, RECONSTRUCTED PHYLOGENY AND GEOGRAPHICAL HISTORY OF THE NEW WORLD SPECIES OF *COPTODERA* DEJEAN (COLEOPTERA: CARABIDAE: LEBIINI)

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Abstract *Proc. ent. Soc. Ont.* 124: 3-182

Keys, descriptions, and illustrations distinguish the known New World species of *Coptodera* (type species—*Coptodera festiva* Dejean), and each taxon is characterized in terms of structural features of adults, habitat, geographical distribution, chorological affinities, and phylogenetic relationships. Twelve new species are described.

The New World species of *Coptodera* are arranged in eleven groups, sequenced according to the reconstructed phylogeny: *C. sallei* group, including *C. sallei* new name; *C. elongata* group, including *C. elongata* Putzeys, *C. schaumi* Chaudoir, *C. megalops* Bates, *C. championi* Bates, and *C. apicalis* new species (type locality—Ecuador, Esmeraldas, Zapallo Grande); *C. aurata* group, including *C. xanthopleura* Bates, *C. aurata* Chevrolat, and *C. viridis* new species (type locality—México, Colima, near Ixtapa); *C. depressa* group, including *C. depressa* Dejean and *C. versicolor* Bates; *C. transversa* group, including *C. dromioides* (Bates), *C. nigrosignata* (Chaudoir); *C. fulminans* (Bates), *C. nigrostriata* (Reiche), *C. lineata* (Bates), *C. stockwelli* new species (type locality—Panamá, Canal Zone, Madden Forest), *C. transversa* (Reiche), *C. sigillata* new species (type locality—Brazil, Santa Catarina, Nova Teutonia), and *C. squiresi* (Chaudoir); *C. festiva* group, including *C. sahlbergi* Chaudoir, *C. relucens* Bates, *C. poecila* Bates, *C. pakitza* new species (type locality—Peru, Madre de Dios, Pakitza), *C. festiva* Dejean, *C. foveolata* new species (type locality—México, Veracruz, Tebanca), *C. nigroviridis* new species (type locality—México, Chiapas, Parque Montebello), *C. rufescens* Buquet, and *C. teutonica* new species (type locality—Brazil, Santa Catarina, Nova Teutonia); *C. aeneorufa* group, including *C. aeneorufa* Bates; *C. bifasciata* group, including *C. bifasciata* Putzeys, *C. tripartita* Chaudoir, *C. cupreotincta* Bates, and *C. braziliensis* new species (type locality—Brazil, Santa Catarina, Hansa Humboldt); *C. emarginata* group, including *C. chalcites* Bates, *C. emarginata* Dejean, and *C. acutipennis* (Buquet); *C. picea* group, including *C. picea* Dejean; and *C. aerata* group, including *C. nitidula* (Buquet), *C. brunnea* new species (type locality—United States, Arizona, Cochise County, Guadalupe Canyon), *C. aerata* Dejean, *C. waytkowskii* Liebke, *C. erwini* new species (type locality—Peru, Madre de Dios, Pakitza), and *C. tripunctata* new species (type locality—Peru, Loreto, Cocha Shinguito).

Removed from synonymy with *C. lineata* Chaudoir is *C. nigrosignata* Chaudoir, the name of a valid species.

Ten synonymies are newly proposed with the senior synonym of each combination listed first: *Coptodera* Dejean = *Stenoglossa* Chaudoir; *C. megalops* Bates = *C. pertzeli* Liebke = *C. peruana* Liebke; *C. depressa* Dejean = *C. plaumanni* Liebke; *C. sahlbergi* Chaudoir = *C. discicollis* Chaudoir; *C. festiva* Dejean = *C. chloris* Bates; *C. cupreotincta* Bates = *C. tesselatus* Chaudoir; *C. acutipennis* (Buquet) = *C. scintillans* Bates; *C. picea* Dejean = *C. unicolor* Chevrolat; *C. nitidula* (Buquet) = *C. triangularis* (Buquet) = *C.*

nubiculosa Chaudoir = *C. flavodisca* Chaudoir; *C.lineata* (Bates) = *C. nigrosignata* (Chaudoir); and *C. transversa* (Reiche) = *C. picturata* (Chaudoir) = *C. undulata* (Chaudoir).

One replacement name is proposed for a junior homonym: *C. sallei* for *C. variegata* Chaudoir.

Six species are removed from *Coptodera* and placed into other genera in the following new combinations: *Microlestodes marcida* Blackburn, *Anchista philippinensis* Jedlička, *Stenognathus robustus* Bates, *Lelis polygona* Bates, *Lelis latipennis* Bates, and *Lelis rutila* Bates.

Coptodera fasciolata Macleay is given new status as the previously used name, *C. aurata* Macleay, and synonym, *C. tesselatus* Chaudoir (1883), are both junior homonyms of *C. aurata* Chevrolat and *C. tesselatus* Chaudoir (1869) respectively.

Based on analysis of 136 character states representing 55 morphological characters (including color), the postulated phylogenetic relationships of the New World species groups of *Coptodera* are: (*sallei*- [*elongata* + *aurata*]) - (*depressa*- (*transversa* - (*festiva*- (*aeneorufa* - {[*bifasciata* + *emarginata*] + [*picea* + *aerata*]})))). Postulated phylogenetic relationships of the species of each group are provided in the text. Most sequences are short, each such involving development of an apotypic state followed by stasis or reversal, and without continued specialization of the apotypy. However, postulated convergences and reversals are numerous. This latter aspect of character evolution may be a reflection of the seemingly slight ecological differentiation of the genus (almost all species are associated with loosened bark on living or dead tree trunks), with lineages being subjected to the same kinds of selective forces but in different combinations in different areas and under oscillating climatic regimes.

Evolution of the extant New World species of *Coptodera* is postulated to have taken place in the tropics, during the time period Late Cretaceous-Recent. Both South America and Middle America + U.S.A. have distinct species assemblages, with most of the evolution of the *sallei* - *elongata* - *aurata* complex having occurred in Middle America, and most of the evolution of the *depressa* - *aerata* complex having taken place in South America.

The evolution of *Coptodera* seems to have involved 14 invasions of Middle America from South America, and four reverse invasions, from Middle America to South America. The fewer, earlier invasions are postulated to have involved crossing of seaways that isolated South America from Middle America, with the more numerous later invasions having taken place when the northern and southern continents were joined by the present Panamanian land connection.

Two lineages, represented respectively by *C. festiva* and *C. picea*, reached the West Indies and southern Florida, probably comparatively recently. Three lineages of the *C. aerata* species group invaded the temperate forests of southern United States: *C. brunnea* and *C. nitidula* did so comparatively recently, and only in the southwest. The ancestral stock of *C. aerata*, the only species of *Coptodera* confined to the North Temperate zone, reached the north at an earlier period.

Because of extensive allopatry and near allopatry of closely related species a general coincidence of geographical range limits and areas of endemism or of refugia (recognized previously on the basis of chorological evidence from plant and other animal taxa), the causes of differentiation of *Coptodera* are to be sought in the general context of tropical forest refuge theory, which postulates recurring cycles of range expansion and

contraction. Differentiation is associated with periods of generally unfavorable climate, resulting in extinction of the forest biota over extensive areas, with its survival in geographically isolated areas that provide local more favorable environmental conditions (the refugia).

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Introduction

The New World species of *Coptodera* Dejean have not been revised since Chaudoir (1869). However, Bates also published a taxonomic treatment of *Coptodera* in that same year, but earlier than Chaudoir. Since each had duplicate specimens of a number of species, several of Chaudoir's new species names were subsequently synonymized with those described by Bates. Liebke (1939, 1951) was the most recent taxonomist to describe several additional species.

While studying the species of *Celaenephes* Schmidt-Goebel and *Euproctinus* Leng & Mutchler, an interest in *Coptodera* was developed. The species in the *Coptodera aerata* group have sensory pits on the ventral surface of antennomeres 5-11 (Figs. 1A-1B) similar to those seen in *Celaenephes* and Metallicine Lebiini. This interest was the starting point for the revision of the New World species of *Coptodera.*

History of Classification of *Coptodera*

The genus *Coptodera* had been included in the pericaline assemblage (Pericalides [Lacordaire 1854: 137], "*Coptodera* and allies" [Bates 1869], Coptoderides [Chaudoir, 1869], or Catascopi [Csiki, 1932: 1352]) since this group of lebiines first was recognized by Lacordaire. Bates (1869: 69), in his inimitable natural historian's approach, brought meaning to the diagnostic features of the pericaline assemblage by noting that the flattened body form and elongate mouthparts with nearly straight mandibles were of adaptive significance to insects living and hunting beneath rather tight-fitting bark of dead or dying trees.

Jeannel (1949) organized the pericaline assemblage of previous authors into two units: the Thyreopteridae (p. 1006) in which he included *Pericalus* Macleay, and the subfamily Coptoderitae (p. 924) of family Lebiidae. In doing so, he ignored the marked similarity between the two groups.

Most subsequent authors (Jedlička 1963; Habu 1967; Ball 1975; and Ball and Shpeley 1983) did not follow Jeannel, but included the coptoderine assemblage with the thyreopterines. Basilewsky (1984: 538-543), in his thought-provoking classification of the genera of African-Madagascan Lebiinae, accepted Jeannel's bipartite arrangement of the pericaloids, but ranked them as tribes (Mormolycini = Thyreopteridae; and Pericalini = Coptoderinae), which were placed in juxtaposition to one another. Also, he included *Pericalus* and *Coptodera* in the same tribe.

Hansen (1968) followed Jeannel in recognizing a subfamily Coptoderinae, but did not discuss its affinities, nor did he present his concept of the more inclusive lebiine assemblage.

Ball (1975: 176), Ball and Shpeley (1983: 751) and Basilewsky (1984: 542) agreed that *Pericalus* Macleay and *Coptodera* were closely related, and that they must be classified together, based on synapotypic features of mouthparts and ovipositor. Basilewsky, however, ranked the inclusive group as a tribe, and recognized two subtribes: Coptoderina, to include *Coptodera* and its immediate relatives that Jeannel and Hansen placed in the Coptoderinae; and the Pericalina, to include *Pericalus*, only. Ball, and Ball and Shpeley included *Coptodera* (*sensu latissimi*) in the pericaloid assemblage of genera, within the subtribe Pericalina.

At the generic level, Jeannel (1949: 924) included in *Coptodera* only New World species, distributing the Old World species among eight genera, most of which were proposed by him. Hansen (1968) followed Jeannel, and proposed two additional genera.

Material and Methods

Materials

This study is based on examination of 2901 adult *Coptodera*, including types of most species, 26 adult *Pericalus* Macleay and three adult *Somotrichus* Seidlitz. Some of the material was available in the Strickland Museum, University of Alberta (UASM). Additional material was borrowed from, or deposited in, the following institutions and private collections, noted in the text by the associated codens. Names of curators are provided also.

AMNH Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York, U.S.A. 10024 (L.H. Herman)

BMNH Department of Entomology, British Museum (Natural History), Cromwell Road, London, England SW7 5BD (N.E. Stork)

CAS Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California, U.S.A. 94118 (D.H. Kavanaugh)

CDAE California State Collection of Arthropods, Department of Food and Agriculture, 1220 N. Street, Sacramento, California, U.S.A. 95814 (F.G. Andrews)

CMNC Canadian Museum of Nature, Entomology, P.O. Box 3443, Station D, Ottawa, Ontario, Canada K1P 6P4 (R.S. Anderson)

CMNH Section of Entomology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania, U.S.A. 15213 (R.L. Davidson)

CNC Canadian National Collection, Biosystematics Research Institute, Agriculture Canada, K.W. Neatby Building, Ottawa, Ontario, Canada K1A 0C6 (Y. Bousquet)

CUIC Department of Entomology, Comstock Hall, Cornell University, Ithaca, New York, U.S.A. 14850 (J.K. Liebherr)

DAPC Darren A. Pollock, Department of Entomology, University of Alberta, Edmonton, Alberta, Canada T6G 2E3

DEUN Division of Entomology, University of Nebraska State Museum, University of Nebraska, Lincoln, Nebraska, U.S.A. 68503 (B.C. Ratcliffe)

DHK David H. Kavanaugh, Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California, U.S.A. 94118

EGRC E.G. Riley, Department of Entomology, Texas A&M University, College Station, Texas, U.S.A.

FMNH Department of Zoology, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois, U.S.A. 60605 (P.P. Parrillo)

FSCA Florida State Collection of Arthropods, Division of Plant Industry, Florida Department of Agriculture, Gainesville, Florida, U.S.A. 32601 (R.E. Woodruff)

GRNC G.R. Noonan, Insect Collection, Milwaukee City Public Museum, 800 West Wells Street, Milwaukee, Wisconsin, U.S.A. 53233

HECO Hope Entomological Collections, University Museum, Parks Road, Oxford, England OX1 3PW (S. Simpson)

HFRE H. Freude, I-60015 Falconara, Via Sadegna 7, Italy

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HNHM Zoological Department, Hungarian Natural History Museum, H-1088 Budapest, Baros u. 13, Hungary (O. Merkl)

HPST H.P. Stockwell, from material on loan from USNM (see below)

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IZWP Instytut Zoologii, Polska Akademia Nauk, 00-679 Warszawa, Poland, ul. Wilcza 64 (S.A. Slipinski)

JAMU Science Museum, Institute of Jamaica, 12-16 East Street, Kingston, Jamaica (T.H. Farr)

JEWC J.E. Wappes, RD 2 Box 16BB, Chadds Ford, Pennsylvania, U.S.A. 19317

JMPR Julio Micheli, 14 Baldorioty St.-Mariani, Ponce, Puerto Rico, U.S.A. 00731

LSUC Louisiana State University Insect Collection, Department of Entomology, Louisiana State University, Baton Rouge, Louisiana, U.S.A. 70803 (V.L. Moseley)

MCSN Museo Civico de Storia Naturale "Giacoma Doria", Via Brigita Ligurua 9, I-16121 Genoa, Italy (R. Poggi)

MCZ Department of Entomology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachussetts, U.S.A. 02138 (S.R. Shaw)

MNHB Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität zu Berlin, 104 Berlin, Invalidenstrasse, D.D.R. (F. Hieke)

MNHP Entomologie, Museum National d'Histoire Naturelle, 45 Rue Buffon, Paris, 75005, France (H. Perrin)

MPEG Departmento de Entomologia, Museu Paraense Emilio Goeldi, C.P. 399, Belem, Para 66000, Brazil.

MPMM Insect Collection, Milwaukee City Public Museum, 800 West Wells Street, Milwaukee, Wisconsin, U.S.A. 53233 (G.R. Noonan)

MSUC Department of Entomology, Michigan State University, East Lansing, Michigan, U.S.A. 48823

MZUM Museum of Zoology, Insect Division, The University of Michigan, Ann Arbor, Michigan, U.S.A. 48109-1079 (M. O'Brien)

MZSP Museu de Zoologie, Universidade de São Paulo, Caixa Postal 7172, São Paulo, Brazil (C. Costa)

OSUC Department of Entomology, Ohio State University, 1735 Neil Avenue, Columbus, Ohio, U.S.A. 43210 (C.A. Triplehorn)

QCAZ Quito Catholic Zoology Museum, Department de Bilogia, Pontificia Universidad Catolica del Ecuador, 12 de Octubre y Carrion, Apto. 2184, Quito, Ecuador

RHTC Robert H. Turnbow, Directorate of Engineering and Housing, Building 1404, Fort Rucker, Alabama, U.S.A. 36362-5137

RTAC R.T. Allen, Department of Entomology, University of Arkansas, Fayetteville, Arkansas, U.S.A. 72701

SEMC Snow Entomological Museum, The University of Kansas, Lawrence, Kansas, U.S.A. 66045-2119 (J.S. Ashe, R. Brooks)

SMC Scott McCleve, 2210-13 Street, Douglas, Arizona, U.S.A. 85607

SPC S.B. Peck, Department of Biology, Carleton University, Ottawa, Ontario, Canada K1S 5B6

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UCBC Division of Entomology and Parasitology, University of California, Berkeley, Berkeley, California, U.S.A. 94720 (J.A. Chemsak)

UCDC The Bohart Museum of Entomology, University of California, Davis, California, U.S.A. 95616

UGCG University of Guatemala Collection, Guatemala City, Guatemala (J. Schuster)

USNM Department of Entomology, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. 20560 (T.L. Erwin)

ZSMM Zoologische Staatssammlung, Münchhausenstrabe 21, D-8000, München 60, Federal Republic of Germany (G. Scherer)

Methods

Taxonomic concepts, principles, criteria for ranking, and general working methods were the same as those previously described (Ball 1975, 1978; Allen and Ball 1980).

Measurements.-- Measurements were made with an ocular micrometer in a Wild M5 stereoscopic microscope, at 12X, 25X or 50X. Measurements of body parts and abbreviations used for them in text and tables are:

Length of head (Hl) - linear distance from base of left mandible to posterior margin of left compound eye;

Width of head (Hw) - maximum distance across the head, including the compound eyes;

Length of pronotum (Pl) - linear distance from anterior to posterior margin, measured along the midline;

Maximum width of pronotum (Pw) - greatest linear transverse distance;

Length of elytra (El) - linear distance from basal ridge to apex of longer elytron, measured along the suture.

Standardized Body Length (SBL), used as an index of overall size, is the sum of Hl, Pl, and El.

Preparation of material.-- Dissections were made using standard techniques. Genitalia and other small structures were preserved in glycerine in microvials, pinned beneath the specimens from which they were removed. Larger structures and those that were gold-coated for study with the SEM were glued to cards pinned beneath the specimens from which they were removed.

Photographs of isolated structures were taken with a Cambridge S-150 "Stereoscan" Scanning Electron Microscope (SEM).

Line drawings of selected body parts were prepared using a camera lucida on a Wild M5 stereoscopic microscope. The figures of male genitalia with macrospines on the internal sac are illustrated in such a manner as to give a notion of their orientation. When the base of a macrospine is filled in (black), the reader is looking down on the base. When the base of a macrospine is open (white), the reader is looking at the opposite surface of it (this is the attachment area of the macrospine to the internal sac).

Special maps were prepared for species or species groups whose ranges extended from México to South America. The region from the Isthmus of Tehuantepec, México to the Panamá-Colombia border is enlarged to better illustrate the distribution patterns.

Notes about descriptions.-- To avoid repetition, character states of lower-ranking taxa recorded in the descriptions of higher-ranking taxa are not repeated in the descriptions of the included lower-ranking taxa. Thus, the complete description of a species must be assembled from its taxonomic placement. Such a description can be obtained by reading the descriptions and diagnoses of the sequence of higher-ranking taxa in which the lower-ranking taxon is placed.

Supraspecific ranking.-- Clusters of species are evident, based on features postulated to be synapotypic, and on distribution pattern or chorological similarity. To designate these monophyletic clusters, the informal category "species group" is used. Although a single

supraspecific-infrageneric level is sufficient to accommodate the New World taxa, a general revision of *Coptodera* (*sensu latissimi*) no doubt will reveal additional levels between genus and species. To accommodate these levels, additional supraspecific ranks, such as subgenus and subgroup will be required.

Catalogue citations of species names.-- Catalogue entries noted in the synonymy of the genus *Coptodera* are not repeated in the species' synonymies: Blackwelder (1944); Csiki (1932); Erwin *et al.* (1977); and Leng (1920).

Label data.-- For type material, the data on each label are reported as exactly as is possible. For other material, only the actual locality and depository of specimens are given. Label data about altitude and date of collection are reported in summary fashion under the headings "Notes about habitat" and "Material examined" respectively.

Terms

Terms for structural features

Most of the words used to designate details of structures are found in textbooks of general entomology, or are used by coleopterists, generally. Other words, required to designate particular structures or parts thereof, are not in general use, though they have been used by us in previous publications. We provide information about these words here.

Microsculpture.-- A "*sculpticell*" is the space enclosed on the surface of the cuticle by adjacent microlines of the integumental system of microsculptue (Allen and Ball 1980: 485-486).

Body parts.-- The term "*segment*" is restricted to those body parts that reflect embryonic somites; thus, somite-like portions of the abdomen are referred to as segments. Abdominal segments are designated by Roman numerals corresponding to the respective somites. The first complete sternum is III, and the last one normally exposed is VII. For numbering the genital somites we follow Bils (1976).

Portions of appendages are designated by the suffix "*-mere*", the prefix depending upon the appendage in question: *antenno-*, *palpo-*, *tarso-*, *et cetera.*

Mandibles.-- Acorn and Ball (1991) summarized previous efforts to describe the features of the mandibles of Carabidae and proposed a modified and more complete system of names. The names offered below reflect this general system, as applied to the mandibles of *Coptodera.*

As in other pericalines (cf. Ball 1975), the mandibles of *Coptodera* adults exhibit reductions and losses, compared to more generalized lebiines and members of most other tribes. Table I lists the diagnostic features of the left and right mandibles for each of the *Coptodera* species groups. The mandibles are trigonal, with broad bases and form falcate (Figs. 2-4). Both mandibles are curved medially, apically. Areas are a broad basal or molar area (m), and the more slender tapered terebra (t), terminated in the acute incisor tooth (i). The dorsal surface of the terebra is strigulose (ts), more or less extensively. The occlusal margin basally is terminated by a group of setae, termed basal brush (bb), Ball's (1975: 149) statement to the contrary notwithstanding. A series of ridges and grooves on the ventral surface is exhibited clearly in occlusal aspect, and best described for left and right mandibles, separately. Ventrally, each mandible exhibits an asetose baso-medial ventral groove (vg), and a medio-lateral sensory groove (sg).

The occlusal area of the left mandible in dorsal aspect (Fig. 2A) exhibits: a dorsal supraterebral ridge (str): terebral ridge (tr), terminated in a blunt terebral tooth (tt) that is evident or not. Posterad the terebral tooth is the combined retinacular area (r-m). In most carabid groups, the retinaculum, with its posterior tooth, is distinct from the molar area. Ventrally, the occlusal

TABLE I. Diagnostic features of adult mandibles of New World species groups of *Coptodera* Dejean.

Species Group	TRL/OL[1]	BW/OL[2]	Terebral Strigils	Left Mandible				Right Mandible		
				Terebral Groove	Retinacular Groove	Ventral Groove	Molar Groove	Retinacular Surface	Post. Retin. Area	Terebral Groove
sallei	0.64	0.38	short, not ext. to str[3]	smooth	smooth	present	triang., base broad	smooth	narrow	smooth
aurata	0.64	0.43	short, not ext. to str	smooth	smooth	present	triang., base broad	smooth	narrow	smooth
elongata	0.66	0.39	short, not ext. to str	smooth	finely strigose	present	triang., base broad	smooth	narrow	smooth
depressa	0.64	0.47	short, not ext. to str, shallow	finely strigose	smooth	present	triang., base broad	smooth	narrow	smooth
transversa	0.70	0.40	short, ext. to str	strigose	strigose	present (very small)	linear, base narrow	strigose	widened slightly	strigose
festiva	0.63	0.46	short, not ext. to str	strigose	finely strigose	absent	linear, base narrow	smooth-strigose	widened slightly	strigose
aeneorufa	0.58	0.43	long, ext. to str	strigose	finely strigose	present	linear, base narrow	strigose	widened moderately	strigose
bifasciata	0.63	0.41	short, not ext. to str, shallow	strigose	strigose	present	linear, base narrow	smooth-strigose	widened slightly	strigose
emarginata	0.55-0.58	0.44-0.45	short-long, ext. to str	strigose	finely strigose	present	linear, base narrow	smooth	widened moderately	strigose
picea	0.55	0.52	long, ext. to str	strigose	strigose	present	linear, base narrow	deeply strigose	widened markedly	strigose
aerata	0.59-0.62	0.47-0.49	long, ext. to str	strigose	strigose	present	narrowly triang.	smooth	widened moderately	strigose

[1] TRL/OL: Length of terebral margin/overall length
0.55-0.58, terebra relatively short
0.59-0.62, terebra moderately long
0.63-0.66, terebra elongate

[2] BW/OL: Width at base/overall length
0.38-0.42, molar area relatively narrow
0.43-0.47, molar area relatively intermediate
0.48-0.52, molar area relatively broad

[3] str: Supraterebral ridge

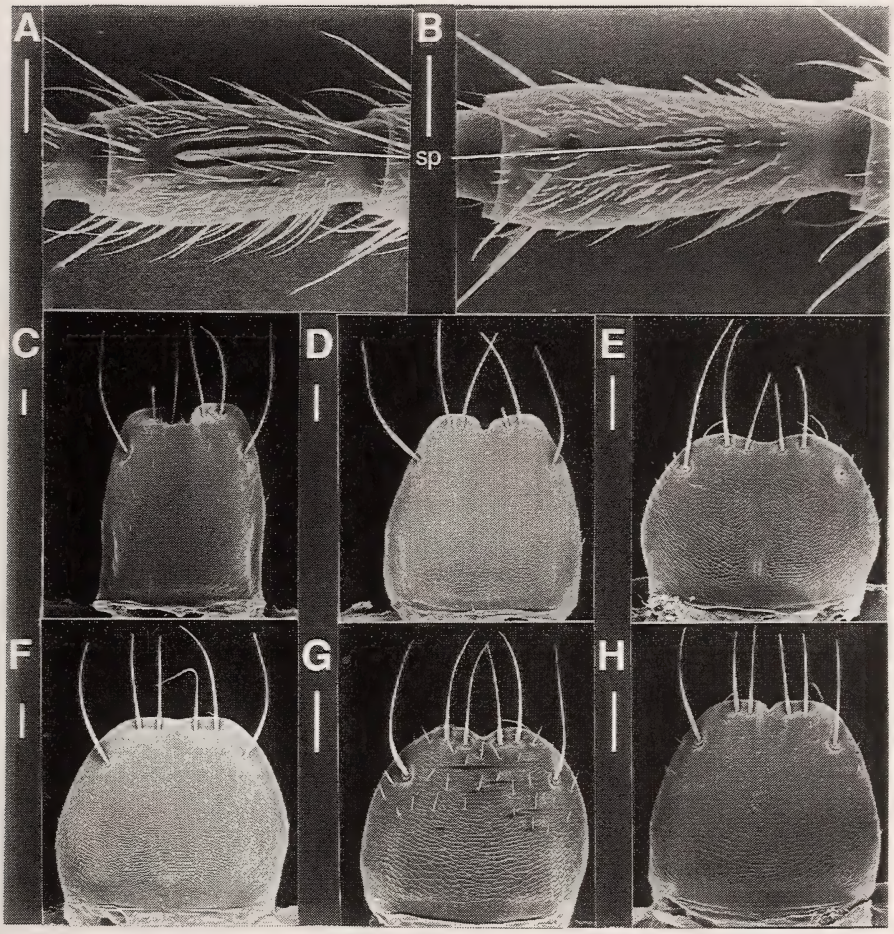


FIGURE 1. SEM photographs of structures of *Coptodera*. Figs. A-B, antennomere 8, ventral aspect. Fig. A: *C. nitidula* (Buquet). Fig. B: *C. brunnea*, new species. Figs. C-H, labrum, dorsal aspect. Fig. C: *C. championi* Bates. Fig. D: *C. xanthopleura* Bates. Fig. E: *C. festiva* Dejean. Fig. F: *C. acutipennis* (Buquet). Fig. G: *C. nitidula* (Buquet). Fig. H: *C. aerata* Dejean. Scale bars: Figs. A-B = 50 μm; Figs. C-H = 100 μm. Legend: sp, sensory pit.

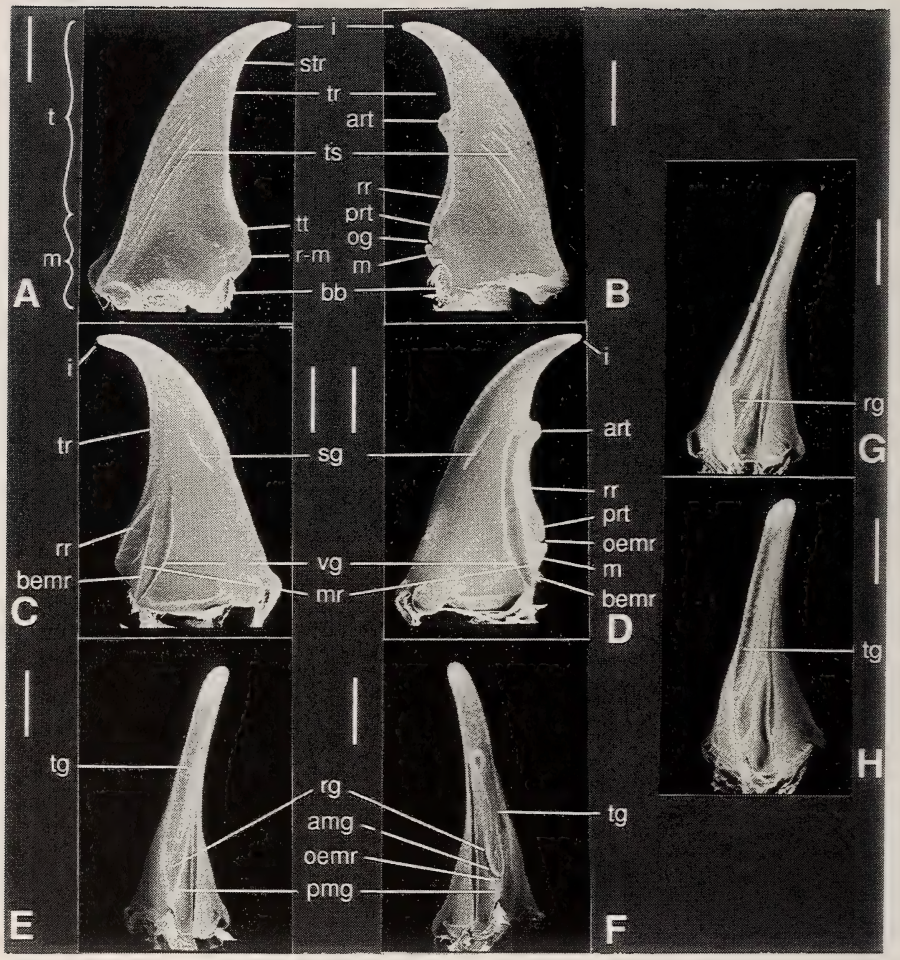


FIGURE 2. SEM photographs of mandibles of *Coptodera* species. Figs. A & C left, dorsal and ventral aspects respectively. Figs. E, G & H left, occlusal aspects. Figs. B, D & F right, dorsal, ventral and occlusal aspects respectively. Figs. A-F: *C. sallei*, new name. Fig. G: *C. championi* Bates. Fig. H: *C. versicolor* Bates. Scale bars = 200 μm. Legend: amg, anterior molar groove; art, anterior retinacular tooth; bb, basal brush; bemr, basal extension of the molar ridge; i, incisor; m, molar area; mr, molar ridge; oemr, occlusal extension of the molar ridge; og, occlusal groove; pmg, posterior molar groove; prt, posterior retinacular tooth; rg, retinacular groove; r-m, retinacular area; rr, retinacular ridge; sg, sensory groove; str, supraterebral ridge; t, terebra; tg, terebral groove; tr, terebral ridge; ts, terebral strigils; tt, terebral tooth; vg, ventral groove.

area includes a retinacular ridge (rr), the sole identifiable remnant of the retinaculum, and a molar ridge (mr), with basal extension (bemr) (In most carabids, an occlusal extension intersects the occlusal margin, marking the separation between molar area and retinaculum).

The occlusal margin of the right mandible exhibits in dorsal aspect (Fig. 2B) a terebral ridge without clear indication posteriorly of a terebral tooth. Ventrad the terebral ridge is the retinaculum, comprising an anterior tooth (art), a ridge (rr), and a posterior portion that is expanded or not (prt). Posteriorly, the molar area (m) is separated from the retinaculum by a shallow groove (og), and an occlusal extension of the molar ridge (oemr). Ventrally, the molar ridge exhibits also a basal extension (bemr).

In occlusal aspect on the left mandible (Fig. 2E), a terebral groove (tg) between suprateretebral and terebral ridges extends the length of the terebra. Posterad the terebral groove is a short triangular depression, the retinacular groove (rg), which, because of the absence of the occlusal extension of the molar ridge, is co-extensive with an anterior molar groove (amg). Posterad the retinacular groove is a posterior molar groove (pmg).

In the occlusal aspect of the right mandible (Fig. 2F) the same grooves as on the left mandible are indicated, but the anterior molar groove and retinacular groove are separated from one another.

Labium.-- The word "*ligula*" is used for glossae + paraglossae. In turn, the fused, sclerotized glossae, characteristic of carabids, are termed collectively the "*glossal sclerite*" (Ball and Shpeley 1983: 746).

Elytra.-- Longitudinal grooves on the dorsal surface (striae of most authors) are designated as "*interneurs*" (Erwin 1974: 3-5), Cooper's (1990) arguments to the contrary notwithstanding.

Male genitalia.-- Median lobes were classified as: anopic (ostium dorsad); catopic (ostium ventrad); pleuropic (ostium lateral and internal sac directed lateral in everted position), left or right. Extent of membranous portion was expressed as length of membranous portion/length of median lobe. Values obtained were classified as follows: short, 0.19-0.28; medium-short, 0.29-0.37; medium, 0.38-0.46; medium-long, 0.47-0.55; and long, 0.56-0.63. Similarly, the apical portion of the median lobe was classified as: very short, 0.02-0.06; short, 0.07-0.10; medium-short, 0.11-0.14; medium, 0.15-0.21; medium-long, 0.22-0.25; and long, 0.26-0.29. These terms were used in the descriptions rather than the actual measurements.

Ovipositor.-- Ball and Shpeley (1983: 746) explain terms used for sclerites and setae, and orientation, of this structure. Note that for the stylomeres, the surfaces that are ventral in the infolded position are lateral when the ovipositor is extended; thus such surfaces are designated as lateral, and the other surfaces are designated accordingly.

Geographical terms

An important landmark that extends north-south in South America is the Andean mountain system. Areas to the west of the Andes are designated *trans*-Andean; those to the east, as *cis*-Andean. The term *Middle America* is used to refer to México + the republics of Central America, collectively. To facilitate zoogeographic discussion, the following terms are used: *Nuclear Middle America*, which includes northern Nicaragua, the Central American republics north thereof and México; *Lower Central America*, which includes the southern part of Nicaragua, Costa Rica and Panamá, a region which, until the Pliocene epoch, consisted of a series of isolated volcanic islands; and *Nuclear Central America*, which includes northern Nicaragua, Honduras, El Salvador and Guatemala, and México south of the Isthmus of Tehuantepec. For South America, two general areas are distinguished: Northern South America, to the north of the Tropic of Capricorn; and Southern South America, to the south of that parallel of latitude. See also Table XV and Map 21 for delimitation of reference areas in South America.

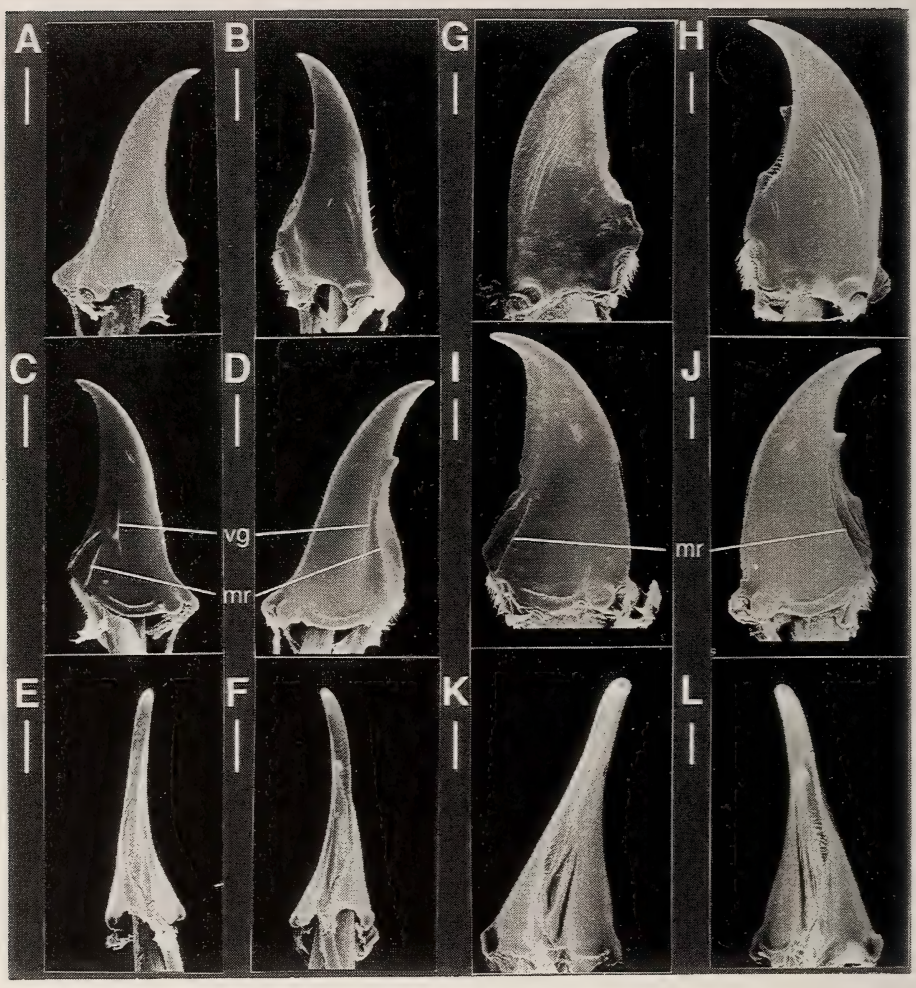


FIGURE 3. SEM photographs of mandibles of *Coptodera* species. Figs. A & G, C & I and E & K left, dorsal, ventral and occlusal aspects respectively. Figs. B & H, D & J and F & L right, dorsal, ventral and occlusal aspects respectively. Figs. A-F: *C. transversa* (Reiche). Figs. G-L: *C. festiva* Dejean. Scales bars = 100 μm. Legend: mr, molar ridge; vg, ventral groove.

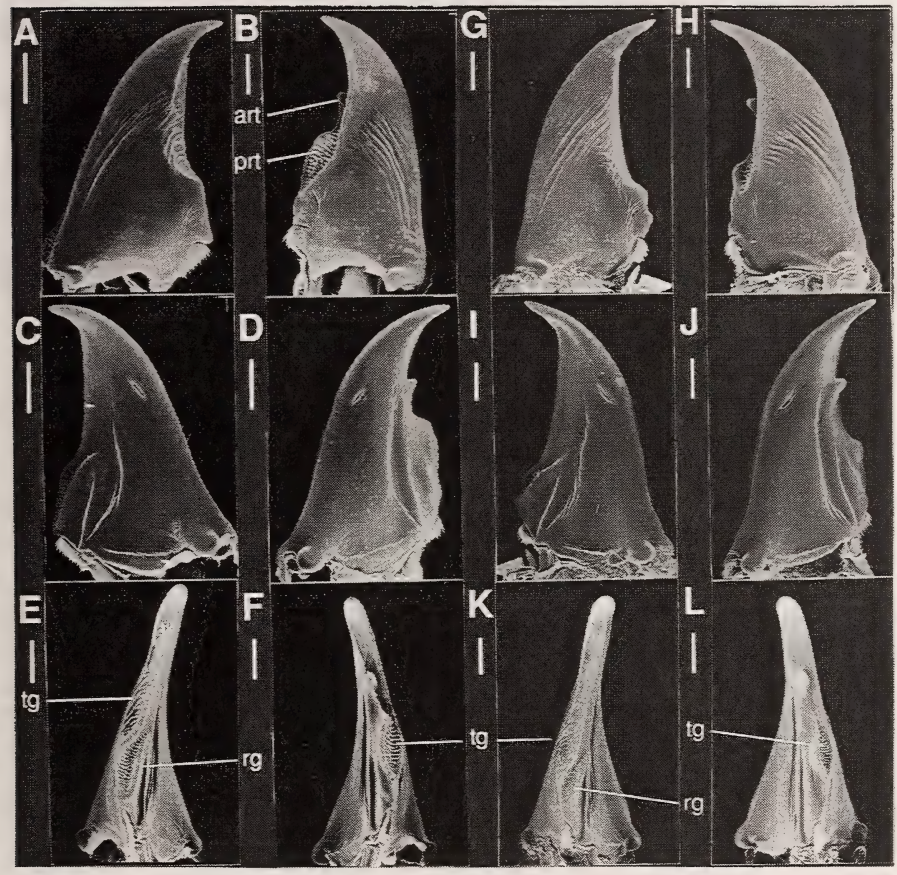


FIGURE 4. SEM photographs of mandibles of *Coptodera* species. Figs. A & G, C & I and E & K left, dorsal, ventral and occlusal aspects respectively. Figs. B & H, D & J and F & L right, dorsal, ventral and occlusal aspects respectively. Figs. A-F: *C. picea* Dejean. Figs. G-L: *C. nitidula* (Buquet). Scales bars = 100 μm. Legend: art, anterior retinacular tooth; prt, posterior retinacular tooth; rg, retinacular groove; tg, terebral groove.

Biogeographical terms

Frank and McCoy (1990) argue that the term "endemic" is restricted most appropriately to its original meaning as a descriptor of populations, the antonym of "epidemic", and implying nothing about native origin. To refer to taxa, they recommend the use of "indigenous" (synonyms: autochthonous, native) for a taxon that achieved its current taxonomic status in the area where it is living. If an indigenous taxon occurs nowhere else, it is referred to as "precinctive" (from Latin, *precinctus*, present participle of *praecingere*, to gird, or encircle).

A taxon that achieved its taxonomic status elsewhere than in a given area where it occurs now, is "adventive" in that area. An adventive taxon is either "introduced" if moved to a given area by man; or it is "immigrant" if it was not introduced.

We find the arguments presented by Frank and McCoy to be cogent and compelling, and adopt here their recommendations.

Phylogenetic terms

Those used are standard, except for "*adelphotaxon*". This word was introduced by Ax (1987: 36) as a substitute for "sister taxon", "sister group". The advantage of using adelphotaxon is that, being of classical origin, it will be the same in all European languages.

Classification

The *Pericalus* Genus-Group

This grouping is equivalent to the Coptoderinae of Jeannel (1949) and Hansen (1968), the "pericaloid assemblage" of Ball and Shpeley (1983: 751), and the tribe Pericalini (Basilewsky 1984: 542).

Recognition.-- This group is characterized by the following features of adults: palpigers setigerous (Fig. 5, each palpiger with one long seta inserted ventrally) and stylomere 2 of the ovipositor (Fig. 12) with very short nematiform setae.

Two genera are included: *Coptodera* Dejean, and *Pericalus* Macleay. Of the two, only *Coptodera* inhabits the New World.

Coptodera Dejean

Coptodera Dejean 1825: 273. TYPE SPECIES: *Coptodera festiva* Dejean 1825: 274. (Subsequent designation, Hope 1838: 85).-- Blanchard 1842: 118, plate 20.-- Duponchel 1844: 202.-- Lacordaire 1854: 140.-- Bates 1869: 71.-- Chaudoir 1869: 163.-- Horn 1881: 156.-- Bates 1883: 180-183.-- Leng 1920: 66.-- Csiki 1932: 1370.-- Darlington 1934: 116.-- Blackwelder 1944: 57.-- Jeannel 1949: 924, 926.-- Ball 1960: 158.-- Habu 1967: 81.-- Darlington 1968: 110.-- Darlington 1971: 194.-- Reichardt 1972: 238.-- Ball 1975: 176.-- Reichardt 1977: 446.-- Erwin & Sims 1984: 398.-- Basilewsky 1984: 542.

Stenoglossa Chaudoir 1848: 116. NEW SYNONOMY. TYPE SPECIES (by monotypy): *Stenoglossa variegata* Chaudoir 1848: 117.-- Lacordaire 1854: 141.-- Bates 1869: 71, 77.-- Chaudoir 1869: 201.-- Bates 1883: 184.-- Csiki 1932: 1375.-- Blackwelder 1944: 58.-- Ball 1975: 172.-- Reichardt 1977: 446.

Haplocrepis Jeannel 1949: 926. NEW SYNONYMY. TYPE SPECIES (original designation): *Coptodera hova* Alluaud 1936: 9.-- Hansen 1968: 346.-- Reichardt 1977: 446.-- Basilewsky 1984: 542.

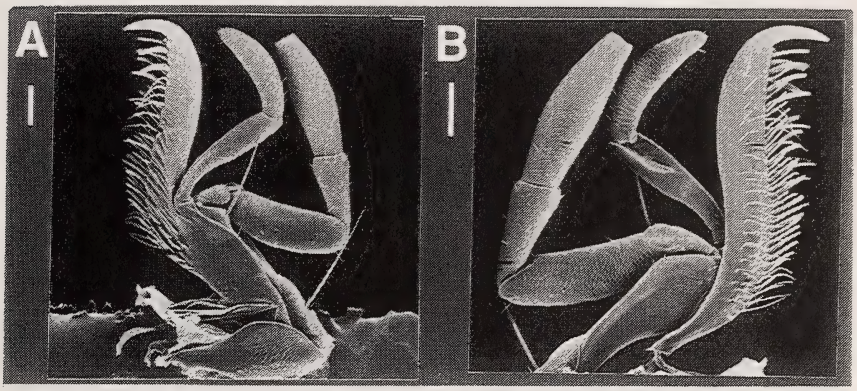


FIGURE 5. SEM photographs of maxilla of *C. sallei*, new name. Figs. A & B dorsal and ventral aspects respectively. Scale bar = 100 μm.

Derivation of generic name.-- From two Greek words: *copto*, cut; and *dere*, neck; in allusion to the straight posterior margin of the pronotum, which seems to have been cut abruptly (Dejean 1825: 273). This is in contrast to the lobed base of the pronotum that is characteristic of *Lebia* adults. Dejean, in proposing *Coptodera*, removed from *Lebia* those species with straight posterior pronotal margins.

Note about type designation.-- Most researchers have listed *Coptodera festiva* Dejean as the type species of *Coptodera* Dejean, a selection made by Hope (1838) and by Duponchel (1844). Blanchard (1842) designated *Coptodera emarginata* Dejean as the type species of *Coptodera* in Plate 20. This designation is invalid by virtue of the principle of priority.

Notes about synonymy.-- Bates (1869: 77-78) noted that specimens of *Stenoglossa* hardly differed from those of *Coptodera* in mouthparts (the basis used by Chaudoir for proposing the former genus), though the lobed base of the pronotum was distinctive. Nonetheless, he wrote that: "Several *Coptoderae* show a trace of the basal lobe, and it is doubtful that the present genus (*i.e. Stenoglossa*) can be maintained. The species have precisely the same habits as the *Coptoderae*." Ball (1975: 172) excluded *Stenoglossa* from the pericaloid assemblage and placed it with the eurycoleoids, though he wrote that: "It is not certain that *Stenoglossa* belongs here..." Although Ball noted the similarity between stylomere 2 exhibited by *Stenoglossa* and *Coptodera* females, he believed the palpigers of the former to be asetose, and so excluded it from the pericaloid assemblage. Basilewsky (1984: 542) suggested that *Stenoglossa* was a pericaloid, even though its palpigers were asetose.

Careful examination showed, in fact, that the palpigers of *Stenoglossa* adults were setigerous. In view of Bates' remarks and our own studies, we are satisfied that *Stenoglossa* and *Coptodera* (*sensu latissimi*) are indeed congeneric.

Jeannel (1949: 926) proposed the genus *Haplocrepis* to accommodate the Madagascan *Coptodera hova* Alluaud, several other Madagascan species, and the Neotropical species *C.*

nubiculosa Chaudoir. The principal character states distinguishing *Haplocrepis* from *Coptodera* were: structure of the median lobe (anopic in *Haplocrepis*), and adult body size (small in *Haplocrepis*). The anopic condition of the male genitalia is likely to be plesiotypic, and thus would not provide good evidence about relationships. Small size is not very convincing, either. Furthermore, *C. nubiculosa* (= *C. nitidula* Buquet) differs from the Madagascan males of *Haplocrepis* by having spines on the internal sac, and by having a much larger apical orifice. It seems doubtful, therefore, that *C. nubiculosa* and *C. hova* belong to the same species group.

More generally, the condition of the median lobe (anopic, pleuropic, catopic) is varied sufficiently among the taxa of the *Pericalus* genus group that such a feature is not a good one to use for making distinctions at the genus level. Concerning *C. nubiculosa*, it belongs to a phylogenetically derived species group of *Coptodera*. For these reasons, the species assigned to *Haplocrepis* by Jeannel and Hansen are regarded as congeneric with those of *Coptodera*.

Diagnosis.-- New World adult *Coptodera* are readily separated from other genera in the subtribe Pericalina by a combination of three character states: mentum without a medial tooth; mandibles not explanate along ventral-lateral margin basally; and labial palpiger setose (Figs. 6A-D).

Limits of the genus.-- We include in *Coptodera* all pericaline taxa with adults characterized by setigerous labial palpigers, and pectinate tarsal claws, *i.e.*, the Coptoderinae of Jeannel (1949) and Hansen (1968), plus various Oriental elements, such as *Lioptera* Chaudoir and *Brachytis* Chaudoir. Because these coptoderine genera are in the Old World, and because the present treatment concerns the New World species only, we have not provided a complete generic synonomy. At some future date, we expect to offer a detailed treatment of the Old World taxa.

Description.-- Form narrow, elongate to moderately wide in relation to length; somewhat flattened to slightly robust. Size various, from small to moderate (SBL 3.80-11.08 mm; Table II).

Color. Dorsal surface dark testaceous to piceous, metallic or not; elytra concolorous, or bicolored, most specimens with pale markings on dark background. Ventral surface, antennae and mouthparts testaceous to rufo-piceous; appendages testaceous to piceous, concolorous or bicolored.

Microsculpture. Microlines of various depth; sculpticells moderately convex to flat. Meshes of labrum, clypeus and head isodiametric; meshes of pronotum isodiametric to moderately transverse, microlines effaced on the disc of some species; meshes of elytra isodiametric to markedly transverse (not iridescent), microlines nearly effaced in some species; meshes of ventral surface isodiametric to markedly transverse (not iridescent), microlines nearly effaced in some species.

Luster. Moderately shining to brilliant, not iridescent.

Fixed setae. As in Lebiini and head with one pair of suborbital setae. Glossal sclerite with two long setae apically. Penultimate labial palpomere bisetose on inner margin near apex; palpiger with a single seta. Disc of elytron with three to four setigerous punctures in third interval. Umbilical series with 14 or more setigerous punctures, setae of different lengths.

Head. Eyes large, subgena markedly reduced. Frons varied, from smooth to markedly wrinkled with longitudinal carinae. Antennomeres 5-11 each with (Figs. 1A-1B) or without sensory pit on ventral surface.

Mouthparts. Labrum (Figs. 1C-1H) elongate to transverse; anterior margin notched medially, or shallowly to deeply emarginate medially. Mandibles (Figs. 2-4) are discussed in detail in the section "Terms for structural features". Maxilla (Fig. 5) average for Lebiini. Labium (Fig. 6) with paraglossae markedly developed; dorsal surface of paraglossae with or without spines.

Prothorax. Pronotum moderately broad (Hw/Pw 0.71-1.21); width greater than length (Pw/Pl 1.38-1.94), widest in anterior half; anterior margin straight to moderately emarginate; lateral

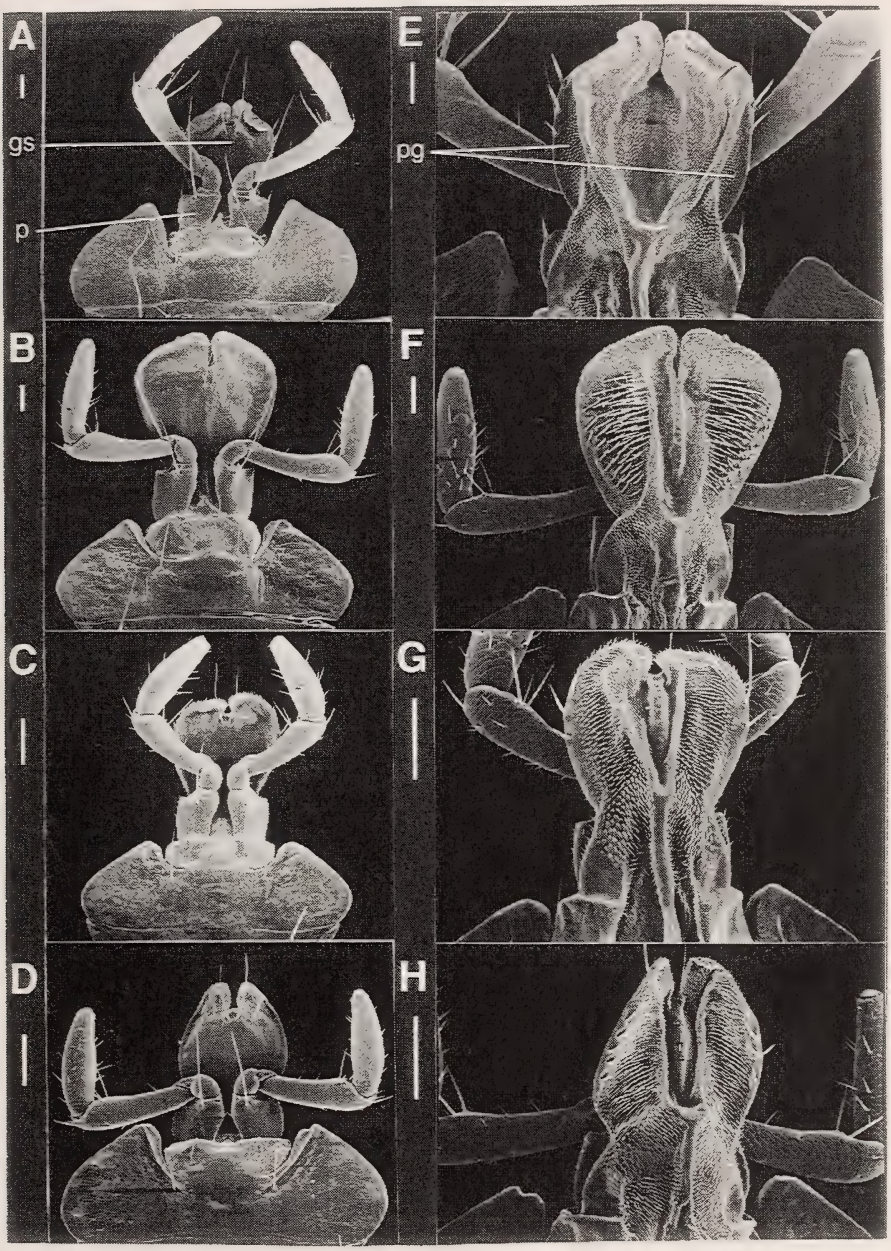


FIGURE 6. SEM photographs of labium of *Coptodera* species. Figs. A-D ventral aspect. Figs. E-H dorsal aspect. Figs. A & E: *C. championi* Bates. Figs. B & F: *C. acutipennis* (Buquet). Figs. C & G: *C. picea* Dejean. Figs. D & H: *C. aerata* Dejean. Scale bars = 100 μm. Legend: gs, glossal sclerite; p, palpiger; pg, paraglossae.

margin slightly rounded, straight or sinuate posteriorly; posterior margin straight (Fig. 7A), slightly convex (Fig. 7C-7D), or lobed (Fig. 7B); hind angles acute to obtuse; disc moderately convex to nearly flat; median longitudinal depression linear, faintly to moderately impressed; lateral grooves narrow to moderately wide; posterior margin beaded. Propleura and prosternum average for Lebiini.

Pterothorax. Average for Lebiini; metepisternum elongate, with lateral margin much longer than width at anterior margin; metepimeron with posterior margin obliquely truncate.

Elytra. Humerus rounded; sides nearly parallel to widened apically; apical margin subtruncate. Apex with lateral and sutural angles spinose or not. Basal ridge complete; lateral margins moderately explanate. Interneurs shallow, punctate to impunctate. Intervals flat to convex.

Hind wings. Fully developed, with large oblongum cell and wedge cell.

Legs. Fore-tibia with markedly reduced to markedly developed upper spur on inner surface. Males with ventral surface of mid-tibia with blunt denticles or notched near apex. Tarsomeres with dorsal surfaces setose. Males with tarsomeres 1-3 of fore-leg with adhesive vestiture, and tarsomeres 2-3 of mid-leg with or without adhesive vestiture. Tarsal claws pectinate, pectens large (Fig. 9H) to small (Fig. 9B).

Habitat range.-- *Coptodera* species were collected at 30 to 2300 m altitude, in most forest types, that range from dry thorn forest to wet cloud forest. Most specimens were taken on standing or fallen tree trunks, living vegetation and also on the ground at fruitfalls.

Relationships.-- *Coptodera* is postulated here to be the adelphotaxon of *Pericalus*.

Classification of the New World species.-- The 43 New World species of *Coptodera* are arranged in 11 species groups (Table I), each postulated to be monophyletic.

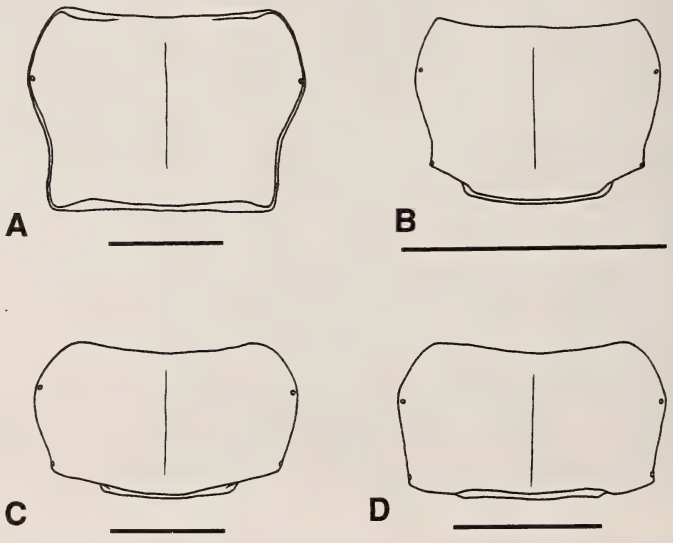


FIGURE 7. Line drawings of pronota of *Coptodera* species, dorsal aspect, lateral setae omitted. Fig. A: *C. apicalis*, new species. Fig. B: *C. stockwelli*, new species. Fig. C: *C. sahlbergi* Chaudoir. Fig. D: *C. teutonica*, new species. Scale bars = 1 mm.

TABLE II. Variation in SBL among males of *Coptodera* Dejean.

Species	Country	N	Range	Mean
C. sallei, new name	México	5	6.33-7.25	6.82
C. elongata Putzeys	México	10	9.42-11.00	9.98
C. schaumi Chaudoir	Costa Rica	4	8.25-9.00	8.79
C. megalops Bates	Bolivia	10	6.58-9.25	8.22
C. championi Bates	Panamá	10	7.25-8.92	8.17
C. apicalis, new species	Colombia	4	6.83-9.00	7.58
	Ecuador	10	7.50-9.75	8.64
C. xanthopleura Bates	México	10	5.68-7.40	6.28
C. aurata Chevrolat	México	9	6.28-7.52	7.03
C. viridis, new species	Panamá	7	6.08-7.42	6.57
C. depressa Dejean	Brazil	10	6.83-8.33	7.87
C. versicolor Bates	Brazil	3	6.25-7.75	7.19
	Peru	3	7.67-7.92	7.81
C. dromioides Bates	Brazil	6	3.50-3.94	3.75
C. nigrosignata Chaudoir	Brazil	4	2.66-3.22	2.99
C. fulminans Bates	Brazil	2	3.14-3.36	3.25
C. nigrostriata Reiche	Bolivia	2	3.46-3.66	3.56
	Brazil	4	3.30-3.92	3.63
C. lineata Bates	México	10	2.76-3.04	2.92
C. stockwelli, new species	Panamá	10	3.08-3.42	3.20
C. transversa Reiche	México	10	2.76-3.02	2.93
C. sigillata, new species	Brazil	1	3.80	3.80
C. sahlbergi Chaudoir	Brazil	4	5.32-6.20	5.81
C. relucens Bates	Brazil	2	5.72-5.84	5.78
C. poecila Bates	Panamá	1	4.64	4.64
C. festiva Dejean	México	10	4.80-5.96	5.13
C. foveolata, new species	México	2	4.84-5.72	5.28
C. nigroviridis, new species	México	1	6.88	6.88
C. rufescens Buquet	Brazil	1	9.33	9.33
C. teutonica, new species	Brazil	1	5.44	5.44
C. aeneorufa Bates	Brazil	6	5.33-6.50	6.04
C. bifasciata Putzeys	Brazil	2	5.88-5.92	5.90
C. tripartita Chaudoir	Brazil	5	5.28-5.88	5.64
C. cupreotincta Bates	Panamá	10	5.83-7.08	6.68
C. braziliensis, new species	Brazil	4	6.42-7.00	6.71
C. chalcites Bates	Brazil	6	6.58-8.83	7.82
	Peru	8	6.92-8.42	7.56
C. emarginata Dejean	Brazil	5	8.75-9.67	9.15
C. acutipennis Buquet (see Table VIII)				
C. picea Dejean	México	10	4.60-5.20	4.91
C. nitidula Buquet	Ecuador	10	4.16-5.40	4.61
C. brunnea, new species	U.S.A.	10	5.36-6.28	5.85
C. aerata Dejean	U.S.A.	10	4.96-5.68	5.35
C. waytkowskii Liebke	Brazil	3	5.32-5.76	5.48

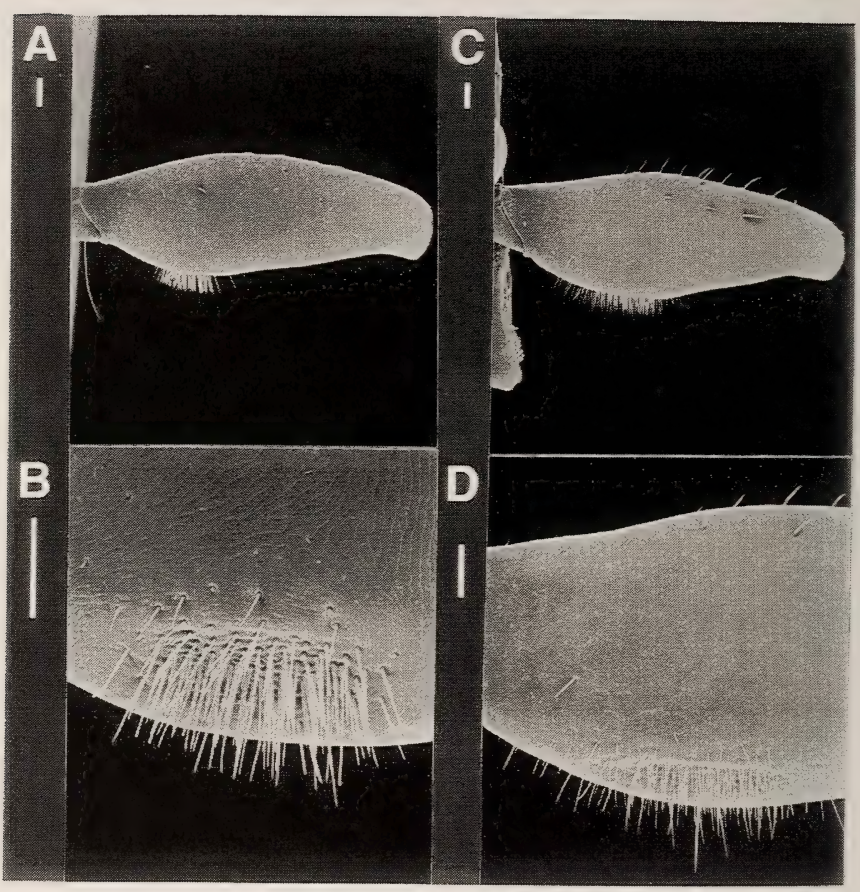


FIGURE 8. SEM photographs of fore-femur of *Coptodera* species, posterior aspect. Figs. A-B: *C. sallei*, new name. Figs. C-D: *C. versicolor* Bates. Scale bars = 100 μm.

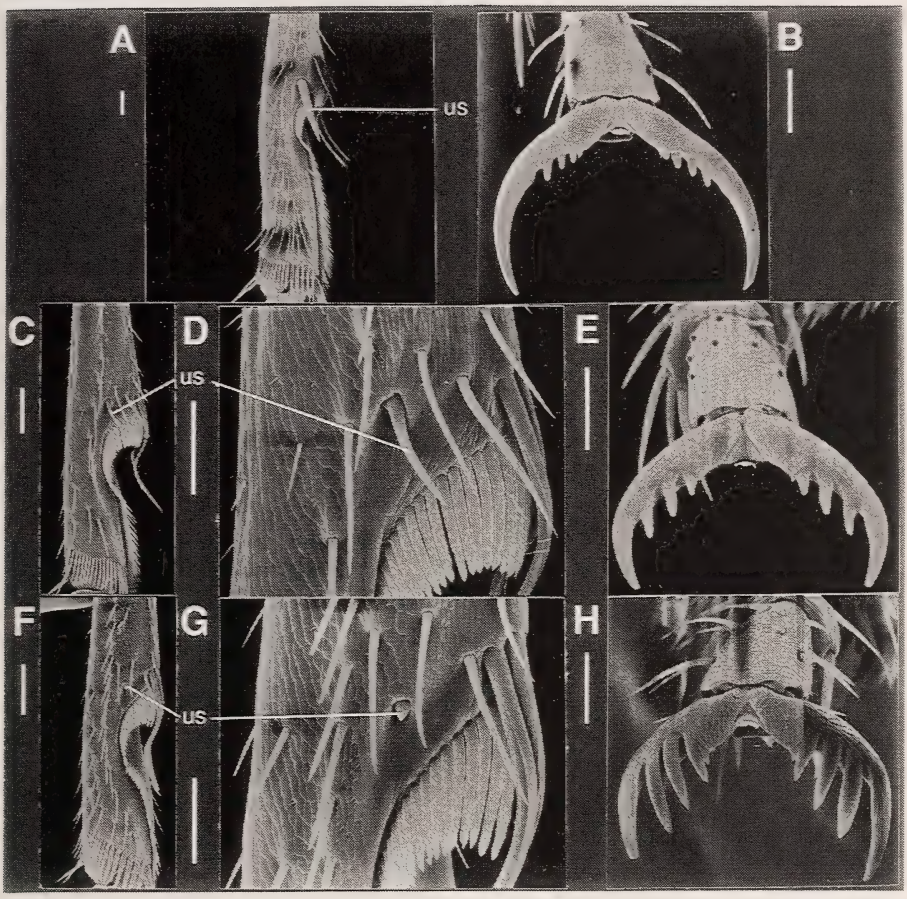


FIGURE 9. SEM photographs of structures of *Coptodera* species. Figs. A, C, D, F & G foretibia, posterior aspect. Figs. A: *C. championi* Bates. Figs. C-D: *C. picea* Dejean. Figs. F-G: *C. nitidula* (Buquet). Figs. B, E & H tarsal claws, terminal aspect. Fig. B: *C. championi* Bates. Fig. E: *C. picea* Dejean. Fig. H: *C. nitidula* (Buquet). Scale bars: Figs. A-C & F = 100 μm; Figs. D, E, G & H = 50 μm. Legend: us, upper spur.

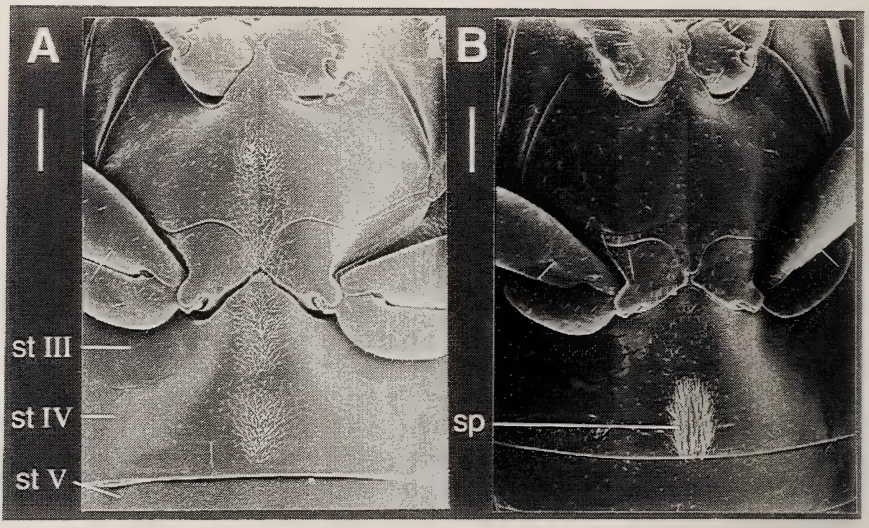


FIGURE 10. SEM photographs of abdominal sterna of *Coptodera* species, ventral aspect. Fig. A: *C. nigrostriata* (Reiche). Fig. B: *C. transversa* (Reiche). Scale bars = 200 μm. Legend: sp, setal patch; st, sternum.

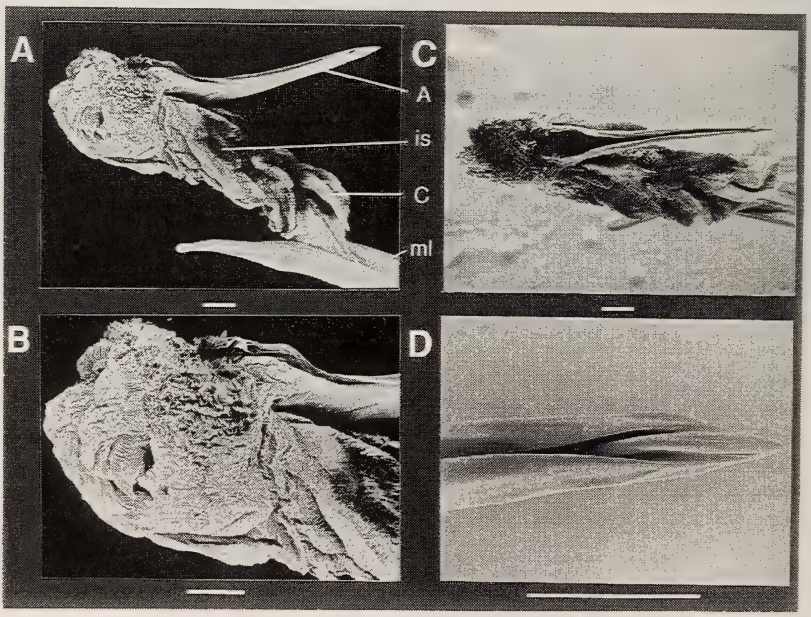


FIGURE 11. SEM photographs of male genitalia of *C. acutipennis* (Buquet), morph J. Fig. A & C and B internal sac, right lateral and dorsal aspects respectively. Fig. D apex of spine A, dorsal aspect. Scale bars = 100 μm. Legend: A, spine A; C, spine C; is, internal sac; ml, median lobe; sp, spine.

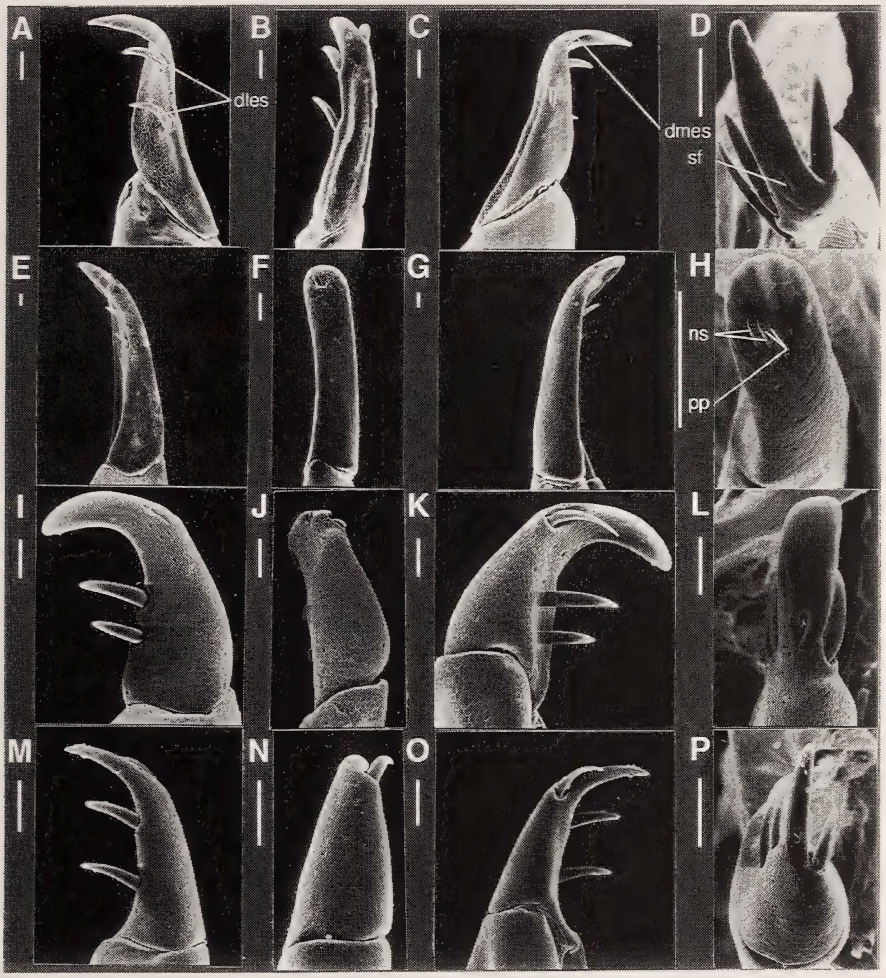


FIGURE 12. SEM photographs of stylomere 2 of ovipositor of *Coptodera* species. Figs. A, E, I & M lateral aspects. Figs. B, F, J & N ventral aspect. Figs. C, G, K & O medial aspect. Figs. D, H, L & P apical aspect. Figs. A-D: *C. championi* Bates. Figs. E-H: *C. transversa* (Reiche). Figs. I-L: *C. rufescens* Buquet. Figs. M-P: *C. aerata* Dejean. Scale bars = 50 μm. Legend: dles, dorsolateral ensiform setae; dmes, dorsomedial ensiform setae; ns, nematiform setae; pp, pit pegs; sf, sensory furrow.

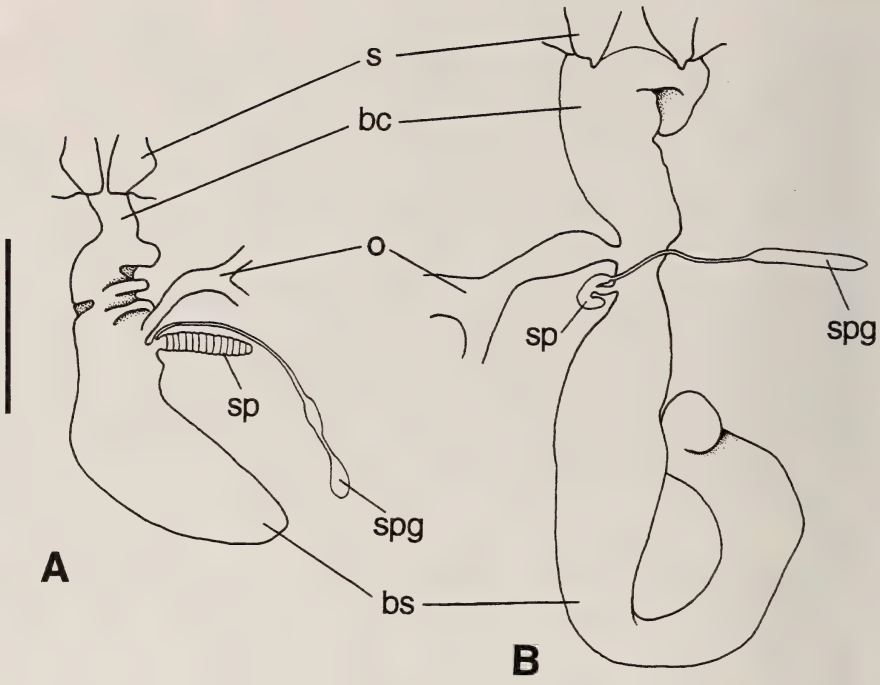


FIGURE 13. Line drawings of female reproductive tract, ventral aspect. Fig. A: *C. elongata* Putzeys. Fig. B: *C. acutipennis* (Buquet). Scale bars = 1 mm. Legend: bc, bursa copulatrix; bs, blind sac; o, oviduct; s, base of stylomere 1; sp, spermatheca; spg, spermathecal gland.

Abdominal sterna. Average for Lebiini. Sternum III and IV with or without scattered or dense setal patches. Sternum VII of males and females with 2 pair of apical setae; apical margin broadly rounded, shallowly notched, or deeply notched.

Male genitalia. Median lobe catopic, pleuropic (hemiopic left or right), or anopic. Internal sac with or without macro spines. "Sperm pump" sclerite associated with the ejaculatory duct.

Ovipositor (Fig. 12). Stylomere 2 about subfalcate, base not lobed; apex of S2 broadly rounded or narrowed. Ensiform setae moderately long, one dorsomedial and two or three dorsolateral; nematiform setae short or absent.

Female genitalia (Fig. 13). Spermatheca very short to longer. "Blind sac" present as small bulge to elongate or bulbous, or not present. [Liebherr (1986: 7) assumes this asymmetric lobe of the bursa copulatrix to be an egg holder in *Agonum* Bonelli].

Geographical distribution.-- The range of *Coptodera* extends throughout the tropics of the world, and warm temperate areas of the New World, and of Eastern Asia. In the New World, *Coptodera* ranges from northern Argentina in cis-Andean South America to southern Michigan and Delaware, in eastern United States (Maps 1-20).

Key to Adults of Species of *Coptodera*

1		Elytron with 3 discal setigerous punctures in interval 3 2
1'		Elytron with 4 discal setigerous punctures in interval 3 15
2	(1)	Elytron with apico-sutural angle spinose 3
2'		Elytron with apico-sutural angle rounded or acute, but not spinose 6
3	(2')	Apical pale markings of elytron longer than basal pale markings (Fig. 15E) . . . . . *C. apicalis*, new species, p. 45
3'		Apical pale markings of elytron similar or shorter than basal pale markings 4
4	(3')	Elytron with basal pale marking of interval 4 as two distinct pale spots (Fig. 15D) . . . . . *C. championi* Bates, p. 45
4'		Elytron with basal pale marking of interval 4 as one long pale spot 5
5	(4')	Elytron with basal pale marking of interval 5 as two distinct pale spots (Fig. 15B) . . . . . *C. schaumi* Chaudoir, p. 38
5'		Elytron with basal pale marking of interval 5 as one short pale spot (Fig. 15C) . . . . . *C. megalops* Bates, p. 40
6	(2')	Apico-lateral angle of elytron sharply obtuse (Fig. 15A) . . . . . *C. elongata* Putzeys, p. 36
6'		Apico-lateral angle of elytron rounded 7
7	(6')	Antennomeres 5-11 each with ventral sensory pit (as in Fig. 1B) 8
7'		Antennomeres 5-11 without ventral sensory pits 9
8	(7)	Head and pronotum colored the same as elytra; specimen from United States . . . . . *C. aerata* Dejean, p. 118
8'		Head and pronotum rufo-testaceous, elytra piceous; specimen from Peru . . . . . *C. tripunctata,* new species, p. 179
9	(8')	Elytra unicolorous 10
9'		Elytra with variegated color pattern 12
10	(9)	Elytral microsculpture coarser, clearly transverse (sculpticells about 3-4 times as wide as long) . . . . . *C. xanthopleura* Bates, p. 49
10'		Elytral microsculpture fainter, isodiametric to slightly transverse, or nearly effaced, sculpticells not distinguishable 11
11	(10')	Elytral intervals flat; elytral microsculpture nearly effaced, without clear formation of sculpticells . . . . . *C. aurata* Chevrolat, p. 50
11'		Elytral intervals convex; elytral microsculpture isodiametric to slightly transverse . . . . . *C. viridis*, new species, p. 51
12	(8')	Elytron with sutural angle acute . . . . . *C. squiresi* (Chaudoir), p. 73
12'		Elytron with sutural angle rounded 12
13	(12')	Upper spur on inner surface of fore-tibia markedly reduced (as in Fig. 9G) . . . . . *C. transversa* (Reiche), p. 68
13'		Upper spur on inner surface of fore-tibia markedly developed 14
14	(13')	Larger in size (average SBL 6.54 mm); anterior margin of labrum notched medially . . . . . *C. sallei*, new name, p. 32
14'		Smaller in size (SBL 3.80mm); anterior margin of labrum shallowly emarginate medially . . . . . *C. sigillata*, new species, p. 70
15	(1')	Antennomeres 5-11 each with ventral sensory pit (Figs. 1A & 1B) 16
15'		Antennomeres 5-11 without ventral sensory pits 19

16 (14) Head with fine setae between posterior pair of supraorbital setae; elytron with apical pale markings only; tarsal claws each with two teeth . . . . . *C. waytkowskii* Liebke, p. 122

16' Head without setae between posterior pair of supraorbital setae; elytron unicolorous to bicolored (without apical pale markings); tarsal claws each with three or four teeth 17

17 (16') Elytron with basal half pale, apical half piceous (Fig. 33E) . . . . . *C. erwini*, new species, p. 122

17' Elytron unicolorous or with markings different than above 18

18 (17') Antennomeres 5-11 each with elongate ventral sensory pit (Fig. 1A); antennomeres unicolorous . . . . . *C. nitidula* (Buquet), p. 112

18' Antennomeres 5-11 each with short ventral sensory pit (as in Fig. 1B); antennomeres 3 and 4 darker than adjacent antennomeres . . . . . *C. brunnea*, new species, p. 116

19 (15') Apex of elytron with lateral angle sharply obtuse to spinose (Fig. 28B) 20

19' Apex of elytron with lateral angle rounded 21

20 (19) Intervals of elytron flattened; microsculpture of elytron nearly isodiametric; apex of elytron with short sinuation before spinose sutural angle (Fig. 28B) . . . . . *C. emarginata* Dejean, p. 98

20' Intervals of elytron convex; microsculpture of elytron stretched to markedly transverse; apex of elytron at sutural angle not as above . . . . . *C. acutipennis* (Buquet), p. 100

21 (19') Fore-tibia with markedly reduced upper spur on ventral surface . . . . . *C. picea* Dejean, p. 108

21' Fore-tibia with moderately long upper spur on ventral surface 22

22 (21') Labrum deeply notched medially (as in Fig. 1C) 23

22' Labrum shallowly emarginate medially 24

23 (22) Elytral interneurs finely punctulate to impunctate . . *C. depressa* Dejean, p. 53

23' Elytral interneurs with rather large, easily seen punctures . . . . . *C. versicolor* Bates, p. 55

24 (22') Elytra unicolorous 25

24' Elytra with variegated color pattern 26

25 (24) Elytral interneurs impunctate; elytron with apico-sutural angle narrowly rounded, nearly acute . . . . . *C. aeneorufa* Bates, p. 87

25' Elytral interneurs distinctly punctate; elytron with apico-sutural angle broadly rounded (Fig. 28A) . . . . . *C. chalcites* Bates, p. 97

26 (24') Interval 9 of elytron testaceous, with dark spots surrounding the medial umbilical setigerous punctures (Figs. 20D-20F) 27

26' Interval 9 of elytron testaceous or dark with only extreme lateral margin testaceous, without dark spots surrounding the medial umbilical setigerous punctures 29

27 (26) Elytral intervals 2 and 3 with dark transverse marking posteriad of discal seta #3 (Fig. 20E); upper spur on inner surface of fore-tibia markedly reduced . . . . . *C. lineata* (Bates), p. 64

27' Elytral intervals 2 and 3 testaceous posteriad of discal seta #3 (Figs. 20D & 20F); upper spur on inner surface of fore-tibia markedly developed 28

28 (27') Specimen from Colombia or Brazil . . . . . *C. nigrostriata* (Reiche), p. 62

28' Specimen from Panamá . . . . . *C. stockwelli*, new species, p. 66
29 (26') Basal pale markings of elytron extensive, extended from suture to interval 8 (Figs. 20A-20C) 30
29' Basal pale markings of elytron present in interval 1 32
30 (29) Elytron with extensive dark markings (Fig. 20A) . *C. dromioides* (Bates), p. 59
30' Elytron with extensive pale markings (Figs. 20B & 20C) 31
31 (30') Apex of elytron nearly straight; dark markings of intervals 4 and 5 with posterior margins anteriad of discal seta #3 (Fig. 20B) . . . . . *C. nigrosignata* Chaudoir, p. 61
31' Apex of elytron sinuate; dark markings of intervals 4 and 5 extended posteriad of discal seta #3 (Fig. 20C) . . . . . *C. fulminans* (Bates), p. 61
32 (29') Basal pale markings in intervals 4 and 6 of elytron extended to apical pale markings in respective intervals (Fig. 23D) . . . . . *C. poecila* Bates, p. 77
32' Basal and apical pale markings in intervals 4 and 6 of elytron separated by darker median transverse marking 33
33 (32') Tarsal claws long, with short denticulations in basal half only . . . . . *C. rufescens* Buquet, p. 85
33' Tarsal claws shorter, with longer denticulations along length of claw 34
34 (33') Elytral interneurs punctate 35
34' Elytral interneurs impunctate 42
35 (34) Basal pale markings in intervals 6-8 of elytron divided into two, and extended to basal ridge (Fig. 23E) . . . . . *C. pakitza*, new species, p. 78
35' Basal pale markings of elytron not extended to basal ridge 36
36 (35') Basal pale markings in intervals 6 and 7 of elytron elongate (Figs. 26C & 26D) 37
36' Basal pale markings in intervals 6 and 7 of elytron shorter in relative length 38
37 (36) Pronotum with broad testaceous lateral margins; apical pale markings of elytron in intervals 2-8 (Fig. 26C) . . . . . *C. cupreotincta* Bates, p. 92
37' Pronotum unicolorous; apical pale markings of elytron in intervals 2-7 (Fig. 26D) . . . . . *C. braziliensis*, new species, p. 94
38 (36') First basal pale marking in interval 3 or 4 of elytron (Figs. 23A, 23H & 23J) 39
38' First basal pale marking in interval 1 or 2 of elytron 41
39 (38) Specimen from México; pale markings of elytron reduced (Fig. 23H) . . . . . *C. nigroviridis*, new species, p. 84
39' Specimen from South America; pale markings of elytron more extensive (Figs. 23A & 23J) 40
40 (39') Pronotum with base narrower at hind angles, and posterior margin distinctly convex (Fig. 7C) . . . . . *C. sahlbergi* Chaudoir, p. 75
40' Pronotum with base wider at hind angles, and posterior margin nearly straight (Fig. 7D) . . . . . *C. teutonica*, new species, p. 86
41 (37') Specimen from Brazil; disc of pronotum broadly pale medially; pale apical marking in interval 4 of elytron widely separated from basal pale marking in interval 5 (Figs. 23B & 23C) . . . . . *C. relucens* Bates, p. 76

41' Specimen from México; disc of pronotum dark; pale apical marking of elytron in interval 4 narrowly separated from basal pale marking of interval 5 (Fig. 23G) . . . . . *C. foveolata*, new species, p. 83

42 (34') Elytron with anterior margin of basal pale markings in intervals 4 and 6 extended equally, or that of interval 6 nearer basal ridge (Figs. 26A & 26B) 43

42' Elytron with anterior margin of basal pale markings in intervals 4 and 6 unequal, that of interval 4 nearer basal ridge (Fig. 23F) . . . . . *C. festiva* Dejean, p. 82

43 (42) Basal pale markings of elytron not extended laterally past interval 8 (Fig. 26A) . . . . . *C. bifasciata* Putzeys, p. 90

43' Basal pale markings of elytron extended to lateral margin (Fig. 26B) . . . . . *C. tripartita* Chaudoir, p. 91

Coptodera sallei Group

This group has a single species, adults of which have notched anterior margin of labrum which is longer than wide, three discal setigerous punctures on each elytron, elytra with variegated pattern, elytral apices not spined, markedly developed upper spur on the inner surface of the fore-tibia, mid-tibia of male with blunt denticles on the ventral surface near the apex, and the fore-femur of males with a dense brush of setae on the ventral surface. See Table I for features of mandibles. Male genitalia median lobe left pleuropic-catopic, more pleuropic than catopic, membranous portion short; internal sac with row of macrotrichia (Figs. 14B-14C). Ovipositor with ensiform setae of stylomere 2 dorso-lateral (cf. Fig. 12A); nematiform setae present. The geographical range of this group is limited to México and Guatemala, in Middle America (Map 1).

Chorological affinities.-- The range of the *C. sallei* group is broadly overlapped in Nuclear Middle America by that of the *C. elongata* and *C. aurata* groups (Maps 1-5).

Phylogenetic relationships.-- This group is the adelphotaxon of the other groups of the 3-punctate lineage (lineage A, Fig. 35).

Coptodera sallei, new name
Figs. 2A-2F, 5, 8A, 8B, 14A-14C; Map 1

Coptodera variegata Chaudoir 1869: 168. Type material: LECTOTYPE (here selected) male, labelled: ♂; Ex Musaeo Chaudoir (red print); TYPE (red paper); LECTO- TYPE (disc with purple border); Coptodera variegata Chaud LECTOTYPE det. G.E. Ball '72; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: México.

Coptodera sallei, NEW NAME, for *Coptodera variegata* Chaudoir.

Notes about nomenclature.-- *Coptodera variegata* Chaudoir (1869: 168) is a junior secondary homonym of *C. variegata* (Chaudoir 1848: 117) which was originally described as a *Stenoglossa*. According to the International Code of Zoological Nomenclature (Third Edition, Article 60), a replacement name must be provided. As a new name, we propose *Coptodera sallei*, in memory

of Auguste Sallé, and in recognition of his many contributions to knowledge of Neotropical Carabidae.

Comparisons.-- Males of *C. versicolor* also exhibit a dense brush of setae on the ventral surface of the fore-femur (Fig. 8).

Description.-- Character states of the *C. sallei* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Dark ferrugineous to rufo-piceous with greenish to aeneous luster; elytra with testaceous to rufo-testaceous markings; lateral margins of elytra slightly paler; appendages brunneous to rufo-piceous; antennae and mouthparts rufo-testaceous to brunneous; palps with apices testaceous; labrum testaceous laterally towards base.

Mouthparts. Mandibles as in Figs. 2A-2F; maxilla as in Fig. 5.

Elytra (Fig. 14A). Interneurs impunctate.

Male genitalia (Figs. 14B-14C). Median lobe with apical portion medium-short, in lateral-left aspect trianguloid, in dorsal aspect sides parallel; apex narrowly rounded in lateral-left and dorsal aspect.

Notes about habitat.--Specimens were taken in México under bark at altitudes of 1219-1981m.

Geographical distribution (Map 1).-- This species is only known from the Pacific Versant of Guatemala and the Gulf Versant of México.

Chorological affinities and phylogenetic relationships (Fig. 36).-- See these topics for the *C. sallei* group, above.

Material examined.-- We examined 40 specimens, including types, and saw non-type material from the following localities:

GUATEMALA Chimaltenango. Finca Monserrat, w slope V. Acatenango (FMNH); **Quezaltenango**. Cerro Zunil (BMNH)(MNHP).

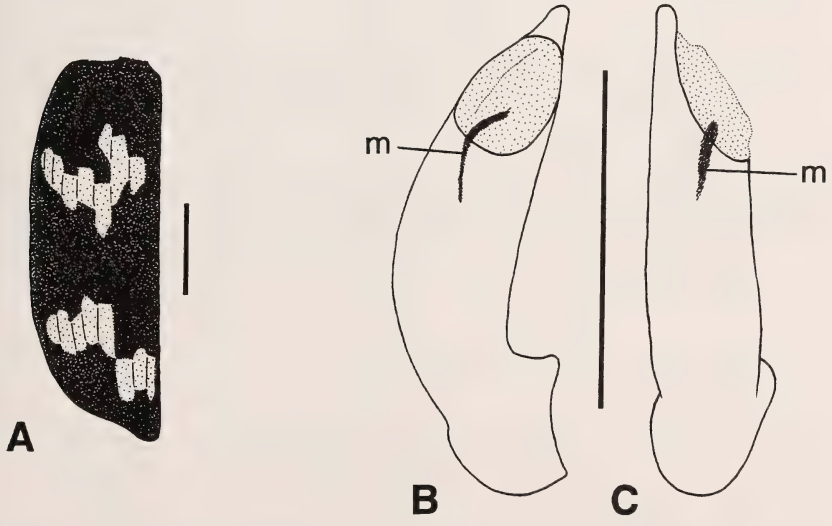
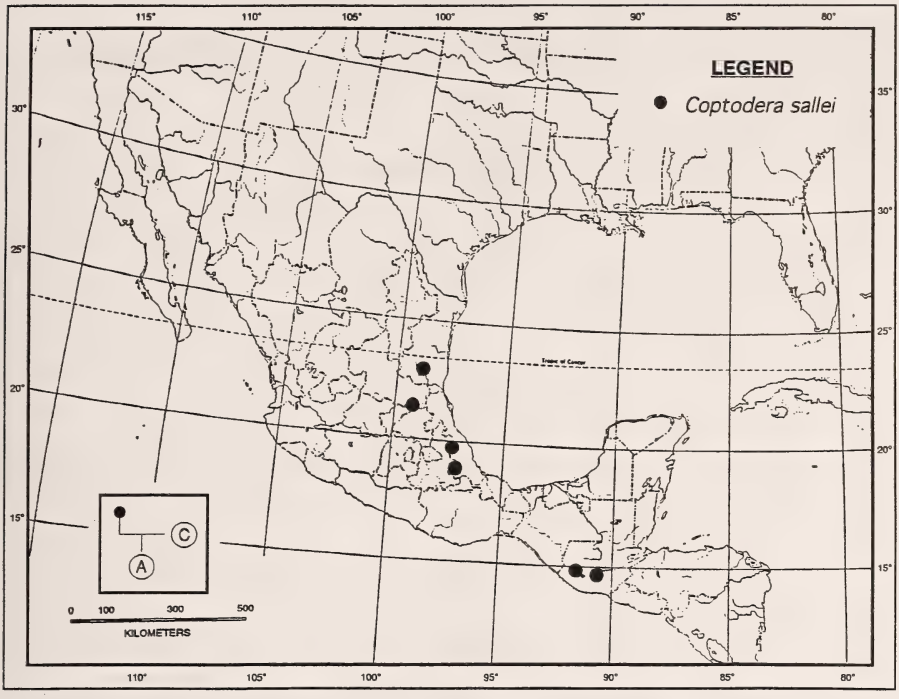


FIGURE 14. Line drawings of structures of *C. sallei*, new name. Fig. A: left elytron, dorsal aspect. Figs. B-C: male genitalia, left lateral and dorsal aspects respectively. Scale bars = 1 mm. Legend: m, microtrichial field.

TABLE III. Variation in SBL among females of *Coptodera* Dejean.

Species	Country	N	Range	Mean
C. sallei, new name	México	5	5.67-6.92	6.27
C. elongata Putzeys	México	10	9.17-10.58	9.84
C. schaumi Chaudoir	Costa Rica	4	8.08-9.42	8.67
C. megalops Bates	Bolivia	8	6.25-8.92	7.90
C. championi Bates	Panamá	10	6.92-8.83	7.73
C. apicalis, new species	Colombia	3	8.25-10.50	9.61
	Ecuador	10	6.83-10.08	8.36
C. xanthopleura Bates	México	10	5.60-6.84	6.10
C. aurata Chevrolat	México	10	6.17-7.67	6.84
C. viridis, new species	Panamá	8	6.17-7.17	6.77
C. depressa Dejean	Brazil	10	6.33-8.50	7.53
C. versicolor Bates	Brazil	3	6.67-7.92	7.28
	Peru	3	6.92-7.50	7.17
C. dromioides Bates	Brazil	5	3.74-3.98	3.90
C. nigrosignata Chaudoir	Brazil	5	3.16-3.40	3.26
C. fulminans Bates	Brazil	2	3.42-3.48	3.45
C. nigrostriata Reiche	Bolivia	3	3.48-3.94	3.65
	Brazil	3	3.50-3.84	3.66
C. lineata Bates	México	10	3.00-3.36	3.20
C. stockwelli, new species	Panamá	10	3.20-3.74	3.50
C. transversa Reiche	México	10	3.06-3.50	3.21
C. squiresi Chaudoir	Brazil	1	4.72	4.72
C. sahlbergi Chaudoir	Brazil	4	5.58-6.88	6.01
C. relucens Bates	Brazil	2	5.48	5.48
C. pakitza, new species	Peru	2	6.00-6.16	6.08
C. festiva Dejean	México	10	4.44-6.16	5.22
C. foveolata, new species	México	1	6.12	6.12
C. nigroviridis, new species	México	1	5.28	5.28
C. rufescens Buquet	Brazil	1	9.42	9.42
C. aeneorufa Bates	Brazil	4	5.75-6.50	6.21
C. bifasciata Putzeys	Brazil	2	5.48-5.56	5.52
C. tripartita Chaudoir	Brazil	5	5.64-5.92	5.77
C. cupreotincta Bates	Panamá	10	6.17-7.33	6.68
C. braziliensis, new species	Brazil	2	6.00-7.17	6.59
C. chalcites Bates	Brazil	2	7.33-9.08	8.21
	Peru	2	6.58-7.42	7.00
C. acutipennis Buquet (see Table VIII)				
C. picea Dejean	México	10	4.32-5.24	4.83
C. nitidula Buquet	Ecuador	10	3.80-5.52	4.46
C. brunnea, new species	U.S.A.	10	5.60-6.28	6.06
C. aerata Dejean	U.S.A.	10	4.60-5.56	5.10
C. erwini, new species	Peru	1	4.36	4.36
C. tripunctata, new species	Peru	1	4.16	4.16



MAP 1. Geographical distribution of *Coptodera sallei*, new name. Inset indicates phylogenetic relationship of species as illustrated in Fig. 36.

MÉXICO (BMNH)(IZWP); **Queretero**. 8.3 km w San Luis Potosí Queretero border, Hwy. 120 (SEMC); **Tamaulipas**. Mun. Gomez Farias, 2 km sw San Jose (TAMU); **Veracruz**. Cordova (BMNH); Jalapa (AMNH)(BMNH)(MCZ)(MNHP). Collections were made in March, May and July.

Coptodera elongata Group

This group has five species with character states as for *C. sallei* group, except the elytral apices of most species are spinose (Figs. 15B-E), the umbilical series of elytron with 16 or more setae, and the fore-femur of males lacks a dense brush of setae on the ventral surface. See Table I for features of mandibles. Male genitalia with median lobe left pleuropic-catopic, more catopic than pleuropic; membranous portion various, medium-short to short; internal sac without macrotrichia or macrospines (Figs. 16A-16J). Ovipositor with ensiform setae of stylomere 2 dorso-lateral (cf. Fig. 12A); nematiform setae absent. The geographical range of this group extends from the Amazon Basin in South America through Central America into México.

Chorological affinities.-- Geographical range overlaps broadly those of the *C. sallei* and *C. aurata* groups (Maps 1-5).

Phylogenetic relationships (Fig. 35).-- This group is the postulated adelphotaxon of the *C. aurata* group.

Coptodera elongata Putzeys
Figs. 13A, 15A, 16A & 16B; Map 2

Coptodera elongata Putzeys 1845: 395. Type material: LECTOTYPE (here selected) female, labelled: ex Musaeo Chaudoir (red print); Museum Paris ex Coll R. Oberthür (light green paper); elongata Putzeys Orizaba Guex & Sallé (original box label)[MNHP]. Type locality: Orizaba, Veracruz, Mexico.-- Chaudoir, 1869: 170.-- Bates 1883: 180.

Description.-- Character states of the *C. elongata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Rufo-piceous to piceous, with greenish luster; elytra with testaceous markings; appendages rufo-piceous; antennomeres 1-4 black, 5-11 brunneous to dark brunneous; mouthparts rufo-piceous; palpomeres with apices testaceous; and labrum testaceous laterally towards base. Ventral surface and femora faintly iridescent.

Fixed setae. Basal lateral setigerous puncture of pronotum in corner of hind angle.

Elytra (Fig. 15A). Interneurs impunctate; apex with lateral angle sharply obtuse and sutural angle rounded.

Legs. Fore-femur and mid-femur of male with numerous and fewer setae respectively on ventral surface.

Male genitalia. Median lobe as in Figs. 16A-16B, with membranous portion short; apical portion in lateral-left aspect short, trianguloid, tapered gradually to apex, in dorsal aspect broader; apex in lateral aspect acute, narrowly rounded, in dorsal aspect more broadly so.

Female genitalia. Reproductive tract as in Fig. 13A.

Notes about habitat.-- In México specimens were taken at altitudes of 30-1372 m; in bromeliads; on downed log with fungus; under bark; and at light. In Guatemala a specimen was taken at 1400-1500 m altitude on logs at night.

Geographical distribution (Map 2).-- The known range of this species extends from the Gulf Versant of México north of the Isthmus of Tehuantepec to Costa Rica, in Lower Central America.

Chorological affinities.-- The range of this species partly overlaps that of *C. schaumi*, but otherwise *C. elongata* is isolated geographically from the other species of the *C. elongata* group.

Phylogenetic relationships (Fig. 36).-- This species is the adelphotaxon of the other species in the *C. elongata* group.

Material examined.-- We examined 119 specimens, including types, and saw non-type material from the following localities:

COSTA RICA Limón. Las Mercedes (MNHP).

GUATEMALA Alto Verapaz. Panzas (=Panzos?)(BMNH); Panzos (MCZ); **Izabel**. San Antonio, 10 km e La Francia (UGCG); **Quezaltenango**. Cerro Zunil (BMNH)(MNHP); **Zacapa**. Sierra del Espiritu Santo, 3 km se La Union (UASM).

MÉXICO (HNHM)(IZWP); **Chiapas**. Lagunas de Montebello Natl. Park, 4 km e Laguna Tziskaw at Dos Lagunas (CAS); **Oaxaca**. 9 km s Valle Nacional, Rte. 175 (UASM); 9.7 km s Valle Nacional (CNC); 12 km s Valle Nacional (CUIC); **Puebla**. Chinantla (BMNH); **Veracruz**. Cordoba (CAS)(UCBC); Fortin de las Flores (CAS)(CNC)(MCZ)(UASM)(UCBC); Jalapa(BMNH);

TABLE IV. Variation in Hw/Pw among males of *Coptodera* Dejean.

Species	Country	N	Range	Mean
C. sallei, new name	México	5	0.81-0.88	0.84
C. elongata Putzeys	México	10	0.90-0.97	0.93
C. schaumi Chaudoir	Costa Rica	4	1.07-1.12	1.10
C. megalops Bates	Bolivia	10	1.06-1.11	1.09
C. championi Bates	Panamá	10	1.11-1.17	1.13
C. apicalis, new species	Colombia	4	1.14-1.21	1.17
	Ecuador	10	1.10-1.18	1.14
C. xanthopleura Bates	México	10	0.91-0.96	0.92
C. aurata Chevrolat	México	9	0.87-0.91	0.89
C. viridis, new species	Panamá	7	0.85-0.92	0.90
C. depressa Dejean	Brazil	10	0.88-0.94	0.91
C. versicolor Bates	Brazil	3	0.87-0.92	0.89
	Peru	3	0.87-0.90	0.89
C. dromioides Bates	Brazil	6	0.92-0.96	0.93
C. nigrosignata Chaudoir	Brazil	4	0.93-0.98	0.96
C. fulminans Bates	Brazil	2	0.93	0.93
C. nigrostriata Reiche	Bolivia	2	0.94-0.95	0.95
	Brazil	4	0.91-0.98	0.95
C. lineata Bates	México	10	0.93-1.00	0.97
C. stockwelli, new species	Panamá	10	0.93-0.95	0.94
C. transversa Reiche	México	10	0.95-1.00	0.98
C. sigillata, new species	Brazil	1	0.90	0.90
C. sahlbergi Chaudoir	Brazil	4	0.73-0.79	0.77
C. relucens Bates	Brazil	2	0.73	0.73
C. poecila Bates	Panamá	1	0.78	0.78
C. festiva Dejean	México	10	0.76-0.81	0.78
C. foveolata, new species	México	2	0.73-0.74	0.74
C. nigroviridis, new species	México	1	0.74	0.74
C. rufescens Buquet	Brazil	1	0.79	0.79
C. teutonica, new species	Brazil	1	0.76	0.76
C. aeneorufa Bates	Brazil	6	0.76-0.85	0.81
C. bifasciata Putzeys	Brazil	2	0.82-0.88	0.85
C. tripartita Chaudoir	Brazil	5	0.83-0.88	0.85
C. cupreotincta Bates	Panamá	10	0.76-0.83	0.79
C. braziliensis, new species	Brazil	4	0.79-0.86	0.82
C. chalcites Bates	Brazil	6	0.79-0.86	0.82
	Peru	8	0.79-0.84	0.82
C. emarginata Dejean	Brazil	5	0.71-0.76	0.73
C. acutipennis Buquet (see Table IX)				
C. picea Dejean	México	10	0.89-0.94	0.91
C. nitidula Buquet	Ecuador	10	0.89-0.94	0.91
C. brunnea, new species	U.S.A.	10	0.89-0.95	0.92
C. aerata Dejean	U.S.A.	10	0.86-0.93	0.89
C. waytkowskii Liebke	Brazil	3	0.88-0.94	0.90

MAP 2. Geographical distribution of *Coptodera elongata* Putzeys. Inset indicates phylogenetic relationship of species as illustrated in Fig. 36.

Est. Biol. Los Tuxtlas (FSCA); Misantla (BMNH); Motzoronga (DEUN); Orizaba (MNHP); Rio Metlac, Fortin de las Flores (UCBC); Rio Metlac Cyn., nw Fortin de las Flores (UCBC); 4 km w Sontecomapan (UASM). Collections are recorded in all months of the year except November.

One specimen (IZWP) labelled "Peru?", which we believe is incorrect.

Coptodera schaumi Chaudoir
Figs. 15B, 16C & 16D; Map 3

Pericalus bifasciatus Schaum 1860: 191. Type material: not seen. Type area: Costa Rica.-- Chaudoir 1861: 123.

Coptodera bifasciata: Chaudoir 1861: 123.

Coptodera schaumi Chaudoir 1861: 123. Replacement name for *C. bifasciata* (Schaum) (*nec* Putzeys).-- 1869: 171.-- Bates 1883: 180.

Notes about type material.-- The type of *P. bifasciata* Schaum was not seen. Schaum's habitus illustration is diagnostic. In the MNHP is a male labelled: Pericalus bifasciatus Schaum (handwritten); Ex Musaeo Chaudoir (red print); TYPE (red paper); Schaumi Chaudoir Costa Rica Stevens (original box label); Museum Paris ex Coll R. Oberthür (light green paper). It is obvious from the labels on this specimen that Chaudoir had seen a specimen of the species for which he

TABLE V. Variation in Hw/Pw among females of *Coptodera* Dejean.

Species	Country	N	Range	Mean
C. sallei, new name	México	5	0.82-0.88	0.85
C. elongata Putzeys	México	10	0.89-0.94	0.92
C. schaumi Chaudoir	Costa Rica	4	1.04-1.10	1.07
C. megalops Bates	Bolivia	8	1.04-1.14	1.09
C. championi Bates	Panamá	10	1.08-1.15	1.13
C. apicalis, new species	Colombia	3	1.09-1.17	1.12
	Ecuador	10	1.11-1.20	1.15
C. xanthopleura Bates	México	10	0.89-0.96	0.93
C. aurata Chevrolat	México	10	0.87-0.92	0.89
C. viridis, new species	Panamá	8	0.89-0.93	0.91
C. depressa Dejean	Brazil	10	0.89-0.94	0.91
C. versicolor Bates	Brazil	3	0.92-0.94	0.93
	Peru	3	0.86-0.90	0.88
C. dromioides Bates	Brazil	5	0.89-0.94	0.92
C. nigrosignata Chaudoir	Brazil	5	0.91-0.95	0.93
C. fulminans Bates	Brazil	2	0.91-0.92	0.92
C. nigrostriata Reiche	Bolivia	3	0.89-0.93	0.91
	Brazil	3	0.89-0.90	0.90
C. lineata Bates	México	10	0.93-0.98	0.96
C. stockwelli, new species	Panamá	10	0.91-0.96	0.93
C. transversa Reiche	México	10	0.95-0.98	0.97
C. squiresi Chaudoir	Brazil	1	0.85	0.85
C. sahlbergi Chaudoir	Brazil	4	0.75-0.77	0.76
C. relucens Bates	Brazil	2	0.76	0.76
C. pakitza, new species	Peru	2	0.78-0.81	0.80
C. festiva Dejean	México	10	0.77-0.84	0.80
C. foveolata, new species	México	1	0.71	0.71
C. nigroviridis, new species	México	1	0.74	0.74
C. rufescens Buquet	Brazil	1	0.84	0.84
C. aeneorufa Bates	Brazil	4	0.79-0.82	0.80
C. bifasciata Putzeys	Brazil	2	0.85-0.88	0.87
C. tripartita Chaudoir	Brazil	5	0.82-0.87	0.85
C. cupreotincta Bates	Panamá	10	0.76-0.83	0.79
C. braziliensis, new species	Brazil	2	0.81-0.85	0.83
C. chalcites Bates	Brazil	2	0.81	0.81
	Peru	2	0.80-0.82	0.81
C. acutipennis Buquet (see Table IX)				
C. picea Dejean	México	10	0.87-0.93	0.91
C. nitidula Buquet	Ecuador	10	0.88-0.97	0.92
C. brunnea, new species	U.S.A.	10	0.89-0.95	0.91
C. aerata Dejean	U.S.A.	10	0.88-0.94	0.92
C. erwini, new species	Peru	1	0.85	0.85
C. tripunctata, new species	Peru	1	0.88	0.88

provided a replacement name. However, this specimen cannot be the type of *P. bifasciata* Schaum as his specimen was collected by M. Wagner rather than by Stevens.

Description.-- Character states of the *C. elongata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum metallic green; elytra rufo-piceous to piceous with greenish to aeneous luster and testaceous markings; appendages, antennae, and mouthparts rufo-piceous; antennomeres 5-11 paler; palps with apices testaceous; labrum testaceous laterally towards base. Ventral surface and femora faintly metallic green.

Fixed setae. Basal lateral setigerous puncture of pronotum anterior of hind angle.

Elytra (Fig. 15B). Interneurs punctate; apex with lateral and sutural angles spinose.

Male genitalia. Median lobe as in Figs. 16C-16D, with membranous portion medium-short; apical portion short, in lateral aspect trapezoidal, in dorsal aspect trianguloid, tapered gradually to apex; apex in lateral aspect obliquely truncate, in dorsal aspect broadly rounded.

Notes about habitat.-- In Costa Rica, specimens were taken at altitudes of 500-700 m; under loose bark of *Enterolobium cyclocarpum* (Jacq.) Griseb. (eardrop tree). In Panamá, specimens were taken at light, both white and uv.

Geographical distribution (Map 3).-- The range of this species extends from the Amazon Basin of Brazil north through Lower Central America to Guatemala in Nuclear Central America.

Chorological affinities.-- The range of *C. schaumi* broadly overlaps that of *C. championi* and to a lesser amount that of *C. elongata*. The ranges of *C. schaumi*, *C. megalops*, and *C. apicalis* are in contact in a narrow zone in Northern South America (Maps 3 and 4).

Phylogenetic relationships (Fig. 36).-- This species is the postulated adelphotaxon of *C. megalops*.

Material examined.-- We examined 73 specimens, including types, and saw non-type material from the following localities:

BRAZIL Amazons (BMNH).

COLOMBIA Chocó. Marzo (MNHP); **?Santander/Boyaca**. Carare (MZSP); **Valle del Cauca/Caldas**. Santa Rosa, entre S. Francisco & Carthago (Etat de Cauca)[sic] (MNHP).

COSTA RICA (BMNH)(CAS)(IZWP)(MNHP)(ZSMM); **Alajuela**. Candelaria Tal. (BMNH); Cariblanco MSUC); **Cartago**. Juan Vinas (DEUN). Turrialba (CAS)(GRNC)(USNM); 3 km se Turrialba (UCBC); **Guanacaste**. Tilaran (OSUC); **Puntarenas**. 4 km n Tarcoles (CAS); **San Jose?**. Piedras Negras (UADE); **?**. Chitaria (USNM). Collections were made in January, March, May, July, August and December.

GUATEMALA (BMNH).

NICARAGUA (BMNH)(MNHP); **Chontales**. (BMNH)(MNHP).

PANAMA Canal Zone. Albrook Forest Site, Fort Clayton (RTAC); Barro Colorado Isl. 9°10'N 79°50'W (USNM); **Chiriqui**. Tolé (BMNH); **Darien**. Santa Fe (OSUC); **Panamá**. Altos (Isla) de Maje 9°08'N 78°49'W (HPST); Bayano Dist., Majé Island (CAS). Collections were made in April to June.

Coptodera megalops Bates
Figs. 15C, 16E & 16F; Map 3

Coptodera megalops Bates 1869: 77. Type material: HOLOTYPE female, labelled: Ega; TYPE (red paper); megalops Bates (handwritten); Ex Musaeo H.W. Bates 1892; Paris Museum ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega, Amazonas, Brazil.

TABLE VI. Variation in Pw/Pl among males of *Coptodera* Dejean.

Species	Country	N	Range	Mean
C. sallei, new name	México	5	1.71-1.93	1.86
C. elongata Putzeys	México	10	1.40-1.56	1.49
C. schaumi Chaudoir	Costa Rica	4	1.42-1.53	1.49
C. megalops Bates	Bolivia	10	1.50-1.58	1.54
C. championi Bates	Panamá	10	1.42-1.53	1.48
C. apicalis, new species	Colombia	4	1.43-1.59	1.49
	Ecuador	10	1.42-1.53	1.47
C. xanthopleura Bates	México	10	1.75-1.85	1.81
C. aurata Chevrolat	México	9	1.81-1.91	1.86
C. viridis, new species	Panamá	7	1.79-1.93	1.85
C. depressa Dejean	Brazil	10	1.69-1.89	1.75
C. versicolor Bates	Brazil	3	1.71-1.82	1.76
	Peru	3	1.72-1.76	1.75
C. dromioides Bates	Brazil	6	1.49-1.58	1.52
C. nigrosignata Chaudoir	Brazil	4	1.37-1.46	1.41
C. fulminans Bates	Brazil	2	1.42-1.43	1.43
C. nigrostriata Reiche	Bolivia	2	1.33-1.40	1.37
	Brazil	4	1.39-1.46	1.42
C. lineata Bates	México	10	1.38-1.50	1.44
C. stockwelli, new species	Panamá	10	1.34-1.44	1.38
C. transversa Reiche	México	10	1.41-1.54	1.47
C. sigillata, new species	Brazil	1	1.49	1.49
C. sahlbergi Chaudoir	Brazil	4	1.69-1.78	1.73
C. relucens Bates	Brazil	2	1.96	1.96
C. poecila Bates	Panamá	1	1.89	1.89
C. festiva Dejean	México	10	1.74-1.90	1.80
C. foveolata, new species	México	2	1.78-1.86	1.82
C. nigroviridis, new species	México	1	1.93	1.93
C. rufescens Buquet	Brazil	1	1.65	1.65
C. teutonica, new species	Brazil	1	1.75	1.75
C. aeneorufa Bates	Brazil	6	1.57-1.79	1.66
C. bifasciata Putzeys	Brazil	2	1.68-1.69	1.69
C. tripartita Chaudoir	Brazil	5	1.68-1.76	1.71
C. cupreotincta Bates	Panamá	10	1.64-1.79	1.72
C. braziliensis, new species	Brazil	4	1.57-1.67	1.62
C. chalcites Bates	Brazil	6	1.44-1.53	1.50
	Peru	8	1.50-1.64	1.55
C. emarginata Dejean	Brazil	5	1.62-1.78	1.71
C. acutipennis Buquet (see Table X)				
C. picea Dejean	México	10	1.60-1.68	1.65
C. nitidula Buquet	Ecuador	10	1.58-1.75	1.67
C. brunnea, new species	U.S.A.	10	1.54-1.67	1.59
C. aerata Dejean	U.S.A.	10	1.65-1.80	1.74
C. waytkowskii Liebke	Brazil	3	1.64-1.67	1.66

Coptodera batesi Chaudoir 1869: 172. Type material: LECTOTYPE (here selected) male, labelled: LECTO (red paper); TYPE (red paper); (green rectangle); Batesi Chaud (handwritten); Ex Musaeo Chaudoir (red print); megalops Bates Amazone Ega Bates (original box label); Coptodera megalops Bates det. George E. Ball '72; Paris Museum ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega (=Tefé), Amazonas, Brazil.-- Bates 1870: XVI.

Coptodera pertzeli Liebke 1951: 242. NEW SYNONYMY. Type material: PARATYPE female, labelled: Peru (handwritten); Sammlg. M. Liebke Eing. Nr. 56, 1932 (green paper); Erworben 1925 aus Sammlg. Oberndorffer Dr. Kallert; Kotype (pink paper); Coptodera pertzeli ♀ M. Liebke determ. Kotype; Inst. Zool. P.A.N. Warszawa 31/54 [IZWP]. Type area: Peru.

Coptodera peruana Liebke 1951: 243. NEW SYNONYMY. Type material: HOLOTYPE male, labelled: Peru (handwritten); Sammlg. M. Liebke Eing. Nr. 56, 1932 (green paper); Erworben 1925 aus Sammlg. Oberndorffer Dr. Kallert (upside down); TYPE (pink paper); Coptodera peruana Lbk. ♂ M. Liebke determ. Type; Inst. zool. P.A.N. Warszawa 31/54 [IZWP]. Type area: Peru.

Notes about synonymy.-- After examining the types of Liebke's species, we believe them to be conspecific with *C. megalops* Bates. Liebke based his two species on forms which had a slightly different elytral color pattern than in the type of *C. megalops*, but these differences are within the range of variation found in *C. megalops*.

Description.-- Character states of the *C. elongata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum metallic green; elytra rufo-piceous to black with greenish to aeneous luster and testaceous markings; appendages, antennae, and mouthparts rufo-piceous; antennomeres 5-11 paler; palps with apices testaceous; labrum testaceous laterally towards base. Ventral surface metallic green; femora faintly metallic green.

Fixed setae. Basal lateral setigerous puncture of pronotum anterior of hind angle.

Elytra (Fig. 15C). Interneurs punctate; apex with lateral and sutural angles spinose.

Male genitalia. Median lobe as in Figs. 16E-16F, with membranous portion medium-short; apical portion medium-short, in lateral aspect trianguloid, very slender, sloped abruptly, in dorsal aspect broader, irregular; apex in lateral aspect very slender, nearly pointed, in dorsal aspect irregular, and broadly rounded.

Notes about habitat.-- Specimens were taken at these altitudes in the following countries: 400-800 m in Bolivia; 430 m in Colombia; 100-250 m in Ecuador; and 290-1200 m in Peru. Specimens were taken under bark of fresh cut tree and in bark and frass in Ecuador; on logs in Peru.

Geographical distribution (Map 3).-- This species' range extends over the upper and middle part of the Amazon Basin in South America.

Chorological affinities and phylogenetic relationships (Fig. 36).-- See topics for *C. schaumi* above, the adelphotaxon of *C. megalops*.

Material examined.-- A total of 174 specimens, including types, was examined. Non-type material was seen from the following localities:

BOLIVIA Cochabamba. Chapare-Gebiet, Oberer Rio Chipiriri (ZSMM); Region Chapare (BMNH)(ZSMM); Villa Tunari (UASM); **Santa Cruz**. (ZSMM). Not located "Ocobamba" (MNHP). Collections were made in February, April, May, August, and October.

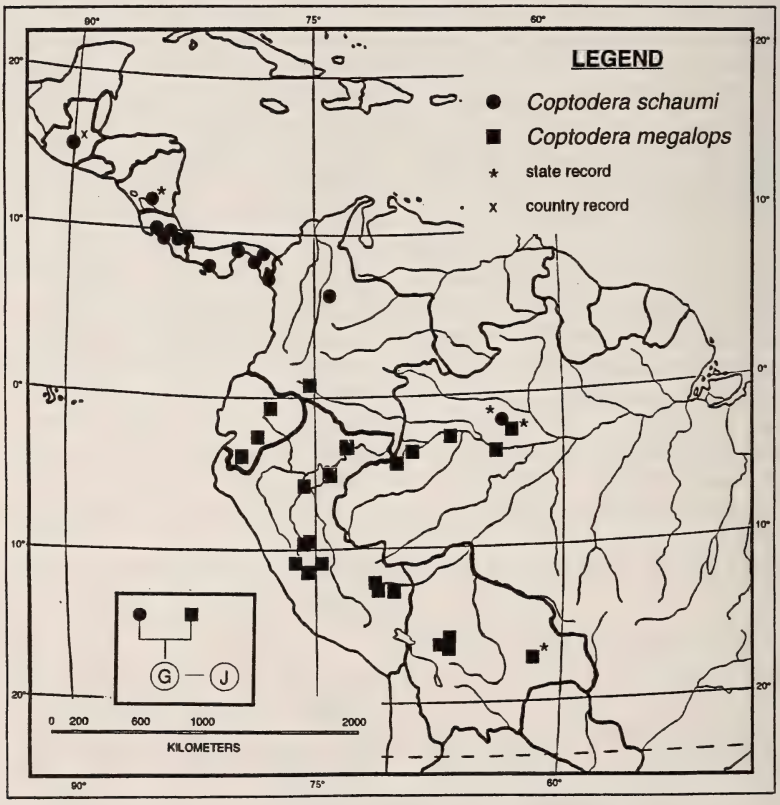
BRAZIL Amazons (BMNH); **Amazonas**. Benjamin Constant, Rio Javary (AMNH); Ega (BMNH)(MNHP); Fonte Boa (BMNH)(MNHP); S. Paulo de Olivença (CMNH). Collections were made in March to May.

TABLE VII. Variation in Pw/Pl among females of *Coptodera* Dejean.

Species	Country	N	Range	Mean
C. sallei, new name	México	5	1.79-1.92	1.87
C. elongata Putzeys	México	10	1.45-1.54	1.51
C. schaumi Chaudoir	Costa Rica	4	1.50-1.53	1.52
C. megalops Bates	Bolivia	8	1.44-1.65	1.57
C. championi Bates	Panamá	10	1.40-1.60	1.49
C. apicalis, new species	Colombia	3	1.50-1.55	1.52
	Ecuador	10	1.43-1.57	1.51
C. xanthopleura Bates	México	10	1.76-1.86	1.81
C. aurata Chevrolat	México	10	1.75-1.94	1.86
C. viridis, new species	Panamá	8	1.73-1.92	1.80
C. depressa Dejean	Brazil	10	1.79-1.94	1.84
C. versicolor Bates	Brazil	3	1.72-1.75	1.73
	Peru	3	1.71-1.87	1.82
C. dromioides Bates	Brazil	5	1.51-1.57	1.53
C. nigrosignata Chaudoir	Brazil	5	1.39-1.44	1.42
C. fulminans Bates	Brazil	2	1.48	1.48
C. nigrostriata Reiche	Bolivia	3	1.44-1.50	1.46
	Brazil	3	1.44-1.49	1.46
C. lineata Bates	México	10	1.37-1.47	1.42
C. stockwelli, new species	Panamá	10	1.39-1.44	1.40
C. transversa Reiche	México	10	1.43-1.57	1.48
C. squiresi Chaudoir	Brazil	1	1.50	1.50
C. sahlbergi Chaudoir	Brazil	4	1.69-1.77	1.73
C. relucens Bates	Brazil	2	1.92	1.92
C. pakitza, new species	Peru	2	1.78-1.82	1.80
C. festiva Dejean	México	10	1.73-1.85	1.80
C. foveolata, new species	México	1	1.86	1.86
C. nigroviridis, new species	México	1	1.91	1.91
C. rufescens Buquet	Brazil	1	1.63	1.63
C. aeneorufa Bates	Brazil	4	1.62-1.71	1.68
C. bifasciata Putzeys	Brazil	2	1.60-1.71	1.66
C. tripartita Chaudoir	Brazil	5	1.63-1.73	1.68
C. cupreotincta Bates	Panamá	10	1.64-1.85	1.72
C. braziliensis, new species	Brazil	2	1.62-1.73	1.68
C. chalcites Bates	Brazil	2	1.55-1.63	1.59
	Peru	2	1.56-1.57	1.57
C. acutipennis Buquet (see Table X)				
C. picea Dejean	México	10	1.61-1.75	1.67
C. nitidula Buquet	Ecuador	10	1.61-1.72	1.64
C. brunnea, new species	U.S.A.	10	1.52-1.67	1.60
C. aerata Dejean	U.S.A.	10	1.67-1.79	1.71
C. erwini, new species	Peru	1	1.65	1.65
C. tripunctata, new species	Peru	1	1.74	1.75

COLOMBIA Caqueta. Morelia, Rio Bodoquero (USNM). Collection was made in January. **ECUADOR** (BMNH); **Loja**. Loja (MNHP); **Napo Pastaza**. Limoncocha (CNC)(UASM); **Santiago-Zamora**. Macas (MNHP). Collections were made in April to August. **PERU** (BMNH); **Huallaga**. Chambireyacù, nr. Yuirimaguas (MNHP); **Huánuco**. Bella Durmiente, nr Tingo Maria (UASM); Cueva de las Pavas Canyon, 8 km s Tingo Maria (FSCA); Monzon Valley, Tingo Maria (CAS); Pozuzo (HNHM)(MNHP); Tingo Maria (AMNH); 69.2 km e Tingo Maria (CAS); vic. Tingo Maria (UKLK); **Junín**. Chanchamayo (HNHM)(MCZ)(MNHP)(USNM); Sani Beni, 8 km e Satipo (SEMC); Satipo (AMNH)(CAS)(MCZ); **Loreto**. Pithecia, 74°05'S 05°02'W (USNM); Rio Napo, Explomapo Camp, Rio Sucusari, 03°15'S 72°55'W (USNM); **Madre de Dios**. Avispas (MCZ); 30 km sw P. Maldonado (USNM); Pakitza, 11°55'48"S 71°35'18"W (USNM); Pakitza, 12°07'S 70°58'W (USNM); Rio Tambopata Reserve, 30 air km sw of Puerto Maldonado (BMNH)(CAS); **Pasco?/Cuzco?**. Quiroz, Rio Paucartambo (MCZ). Not located "**Loreto**. Cavallo-Cocho" (MNHP). Collections were made in April to January.

One specimen labelled "Amazon, or Guatem." (BMNH).



MAP 3. Geographical distribution of *Coptodera schaumi* Chaudoir and *C. megaplops* Bates. Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

Coptodera championi Bates
Figs. 1C, 2G, 6A, 6E, 9A, 9B, 12A-12D, 15D, 16G & 16H; Map 4

Coptodera championi Bates 1883: 180. Type material: LECTOTYPE (here selected) female, one of a pair glued on same card, indicated by a small arrow, labelled: Type H.T. (disc with red border); Bugaba 800-1500' Champion; B.C.A. Col.I.1 Coptodera championi, Bates; Coptodera championi Bates (Bates' handwriting); LECTOTYPE ♀ Coptodera championi Bates By Erwin '76 [BMNH]. Type locality: Bugaba, Chiriqui Prov., Panamá.

Description.-- Character states of the *C. elongata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum metallic green; elytra rufo-piceous to piceous with greenish luster and testaceous markings; lateral margins of pronotum and elytra with cyaneous luster; appendages, antennae, and mouthparts rufo-piceous; terminal palpomeres with apices testaceous; labrum testaceous laterally towards base. Ventral surface and femora metallic blue.

Fixed setae. Basal lateral setigerous puncture of pronotum anterior of hind angle.

Mouthparts. Labrum as in Fig. 1C; left mandible as in Fig. 2G; labium as in Figs. 6A & 6E.

Elytra (Fig. 15D). Interneurs punctate; apex with lateral and sutural angles spinose.

Legs. Fore-tibia with long upper spur on inner surface (Fig. 9A); tarsal claws nearly smooth (Fig. 9B).

Male genitalia. Median lobe as in Figs 16G-16H, with membranous portion short; apical portion short, in lateral aspect broad, hardly tapered, in dorsal aspect similar, hardly tapered; apex in lateral aspect broadly rounded, in dorsal aspect sub-truncate.

Ovipositor. Stylomere 2 as in Figs. 12A-12D.

Notes about habitat.-- In Panamá this species has been taken at altitudes of 150-580 m, on logs, running on log, running on logs or branches at or near fermenting sap, at night, at white and uv lights.

Geographical distribution (Map 4).-- This species is known from Panamá and trans-Andean Colombia.

Chorological affinities.-- The ranges of *C. championi* and *C. apicalis* are adjacent to one another, and may meet in Colombia.

Phylogenetic relationships (Fig. 36).-- This species is the postulated adelphotaxon of *C. apicalis*.

Material examined.-- A total of 128 specimens, including types were examined. Non-type material was seen from the following localities:

COLOMBIA Valle del Cauca. Buenaventura (BMNH); R. Dagua (MNHP).

PANAMA Bocas del Toro. 5 km sw Almirante 9°16'N 82°25'W (USNM); **Canal Zone**. Ciricito (USNM); Madden Forest, Mi 2, 9°05'N 79°37'W (DHK)(HPST); Barro Colorado Isl. 9°10'N 79°50'W (AMNH)(FMNH)(MCZ)(UCDC)(USNM); **Chiriqui**. (HNHM)(MNHP); Bugaba (MCZ)(MNHP)(UASM)(USNM); **Panamá**. Cerro Campana 8°40'N 79°56'W (USNM). Collections were made in January, and May to August.

Coptodera apicalis, new species
Figs. 7A, 15E, 16I & 16J; Map 4

Type material.-- HOLOTYPE male, labelled: ECUADOR:Esm.Pr. Zapallo Grande 4 February 1988 Mike Huybensz [USNM]. ALLOTYPE female, labelled same as holotype [USNM]. 43

additional PARATYPES, sex and label data as follows: 15 males and 11 females same as holotype [BMNH][CAS][FMNH][MNHP][QCAZ][UASM][USNM]. 3 males: ECUADOR Esmeraldas Pr. Zapallo Grande, Oct. 25-39, 1987 Michael Huybensz [CMNH]. 1 male: ECUADOR:Cotopaxi Guasaganda 500m 1 April 1988 Mike Huynesz [UASM]. 1 male: ECUADOR: Carchi Hojal VIII.9.1983 Coll. R. Davidson [CMNH]. 1 male and 2 females: ECUADOR: Carchi Hojal 25 July 1983 R.Davidson & J. Rawlins; running on moss & sheet fungus on large log [CMNH]. 2 females: SantoDomingo Ecuador2-X-50 JWFunkhouser; P. S. Bartholomew Collection Calif. Acad. Sci. Accession 1967 [CAS]. 1 male: 1200', Anchicaya Dam, 70 km E.Buenaventura, Valle,Colombia,VII.22, 1970. H. & A. Howden [UASM]. 1 female: 1200', Anchicaya Dam, 70 km E.Buenaventura, Valle,Colombia,VII.23, 1970. H. & A. Howden [UASM]. 1 male: COLOM.,1000' Anchicaya VII.21.1970 J.M. Campbell [CNC]. 2 females: COLOM.,1000' Anchicaya VII.22.1970 J.M. Campbell [CNC]. 2 males: COLOM.,1500' Anchicaya VII.26.1970 J.M. Campbell [CNC].

Type locality.-- Zapallo Grande, Esmeraldas province, Ecuador.

Derivation of specific epithet.-- From Latin *apex*, in allusion to the elongate pale apical markings on the elytra.

Description.-- Character states of the *C. elongata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum metallic green; elytra rufo-piceous to piceous with greenish to aeneous luster and testaceous markings; lateral margins of pronotum and elytra with cyaneous luster; appendages, antennae, and mouthparts rufo-piceous; terminal palpomeres with apices testaceous; labrum testaceous laterally towards base. Ventral surface and femora metallic blue.

Fixed setae. Basal lateral setigerous puncture of pronotum anterior of hind angle (Fig. 7A).

Elytra (Fig. 15E). Interneurs punctate; intervals 1-4 flat medially, convex in pale apical marking; apex with lateral and sutural angles spinose.

Legs. Tarsal claws nearly smooth.

Male genitalia. Median lobe as in Figs. 16I-16J, with membranous portion short; apical portion short, in lateral aspect broad, tapered slightly, in dorsal aspect similar, hardly tapered; apex in lateral and dorsal aspects broadly rounded.

Notes about habitat.-- Specimens were taken at altitudes of 304-457 m in Colombia and at 500 m in Ecuador; running on moss and sheet fungus on large logs in Ecuador.

Geographical distribution (Map 4).-- This species is known from the Chacó area of trans-Andean Colombia and Ecuador.

Chorological affinities and phylogenetic relationships (Fig. 36).-- See topics for *C. championi* above, the adelphotaxon of *C. apicalis*.

Material examined.-- Type material only; see above for details.

Coptodera aurata Group

This group includes three species with character states of the *C. sallei* group, except the elytra are unicolorous rather than variegated, and the fore-femur of males lacks a dense brush of setae on the ventral surface. See Table I for features of mandibles. Male genitalia with median lobe left pleuropic-catopic, more catopic than pleuropic; membranous portion medium-short; internal sac without macrotrichia or macrospines (Figs. 17A-17F). Ovipositor with ensiform setae of stylomere 2 dorso-lateral (cf. Fig. 12A); nematiform setae present. The geographical range of this group is confined to Middle America, extending from México south to Nicaragua (Map 5).

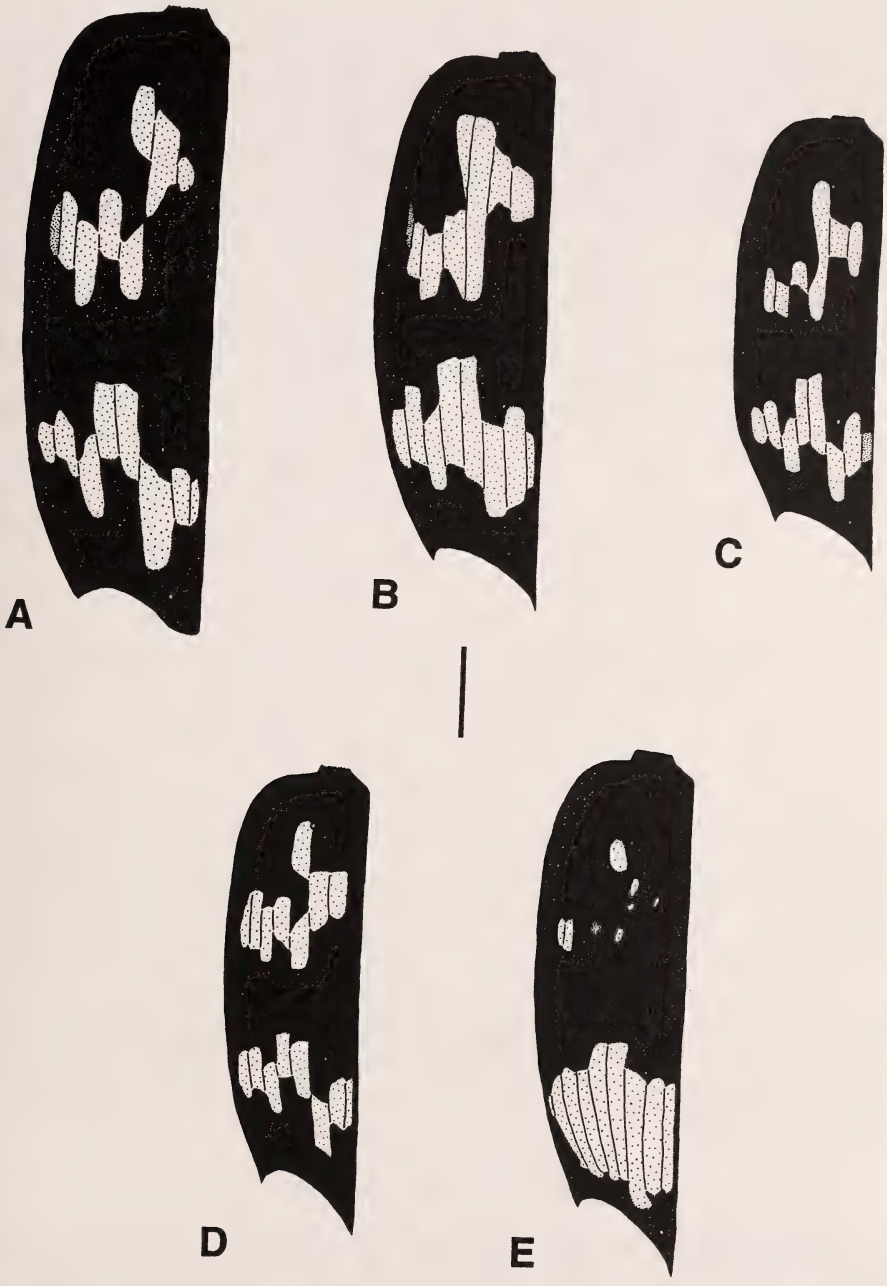


FIGURE 15. Line drawings of left elytron of *Coptodera elongata* group, dorsal aspect. Fig. A: *C. elongata* Putzeys. Fig. B: *C. schaumi* Chaudoir. Fig. C: *C. megalops* Bates. Fig. D: *C. championi* Bates. Fig. E: *C. apicalis*, new species. Scale bars = 1 mm.

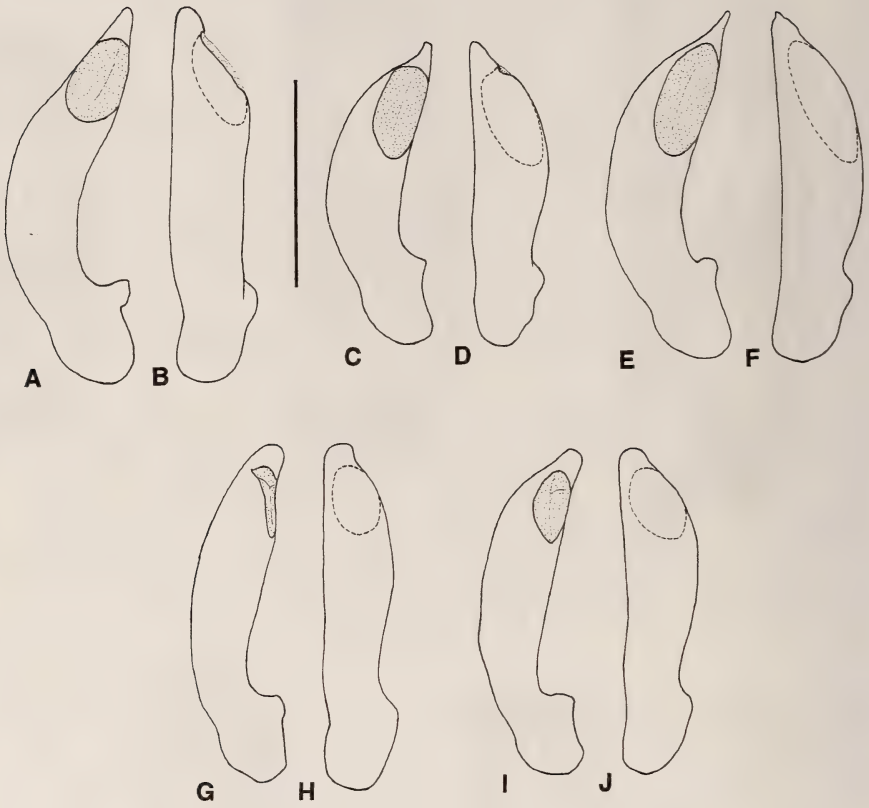


FIGURE 16. Line drawings of male genitalia of *Coptodera elongata* group. Figs. A, C, E, G & I left lateral aspect. Figs. B, D, F, H & J dorsal aspect. Fig. A-B: *C. elongata* Putzeys. Fig. C-D: *C. schaumi* Chaudoir. Fig. E-F: *C. megalops* Bates. Fig. G-H: *C. championi* Bates. Fig. I-J: *C. apicalis*, new species. Scale bars = 1 mm.

Chorological affinities.-- Geographical range of this group is overlapped broadly in Nuclear Middle America by those of the *C. sallei* and *C. elongata* groups (Maps 1-4).

Phylogenetic relationships (Fig. 35).-- This is the postulated adelphotaxon of the *C. elongata* group.

MAP 4. Geographical distribution of *Coptodera championi* Bates and *C. apicalis*, new species. Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

Coptodera xanthopleura Bates
Figs. 1D, 17A & 17B, Map 5

Coptodera xanthopleura Bates 1891: 270. Type material: LECTOTYPE (here selected) female, labelled: Type H.T. (disc with red border); Tehuantepec; Mexico Sallé Coll.; 1891-64; Coptodera xanthopleura Bates (Bates' handwriting) [BMNH]. Type locality: Tehuantepec, Oaxaca, México.

Notes about type material.-- In the MNHP is a female specimen labelled: Dos Arroyos Guerrero 1000 ft. Sept. H.H. Smith; Coptodera xanthopleura Bates (handwritten); Ex Musaeo H.W.

Bates 1892; Museum Paris ex Coll R. Oberthür (light green paper); and is here selected as PARALECTOTYPE.

Description.-- Character states of the *C. aurata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Elytra dark brunneous with faint greenish lustre; head and pronotum darker, faintly to brightly metallic green; lateral margins of elytra testaceous to rufo-testaceous; appendages, antennae, and mouthparts brunneous to dark brunneous; terminal palpomeres with apices testaceous.

Mouthparts. Labrum as in Fig. 1D.

Elytra. Interneurs impunctate.

Male genitalia. Median lobe as in Figs. 17A-17B, with apical portion short, in lateral-left aspect trianguloid, hardly tapered, in dorsal aspect broadly triangular; apex in lateral-left aspect narrowly rounded, more broadly so in dorsal aspect.

Notes about habitat.-- Specimens were taken at altitudes of 30-1500 m; at u-v light; in a tropical riparian forest; from a log in a thorn forest; and from under bark of a dead tree in a gallery forest.

Geographical distribution (Map 5).-- This species is known only from the Pacific Versant of México, from Nayarit (north of the Isthmus of Tehuantepec) to eastern Chiapas (in Nuclear Central America).

Chorological affinities.-- At its northern periphery, the range of *C. xanthopleura* is broadly overlapped by that of *C. viridis*. Southward, in Nuclear Central America, the range of *C. xanthopleura* is in contact with that of *C. aurata*.

Phylogenetic relationships (Fig. 36).-- As shown by genitalic features (Fig. 17), *C. xanthopleura* is the adelphotaxon of the species pair *C. aurata* + *viridis*.

Material examined.-- We examined 55 specimens, including types, and saw non-type material from the following localities:

MÉXICO(HNHM); **Chiapas**. Cinco Cerros, Km 30 on Hwy 190 (UASM); Cd. Cuauhtemoc (UASM); 4.7 & 7.9 km n Frontera Comalapa (UASM); Municipio La Trinitaria, 18 km s of La Trinitaria, small road nw Rte. 190 (CAS); **Jalisco**. nr Ixtapa (UASM); 2 km se Las Palmas (UASM); 33.8 km s Puerto Vallarata (UASM); **Nayarit**. 3 mi n Acaponeta (CDAE); Arroyo Canaveral, nr. Jesus Maria (CAS); Mecatan (AMNH); 9.2 km e San Blas, Rte. 46 (UASM); **Oaxaca**. 5 km e Tavela (UASM); **Sinaloa**. 6-7 km n La Capilla de Taxte (RHTC). Collections in May to July, September, and December.

Coptodera aurata Chevrolat
Figs. 17C & 17D; Map 5

Coptodera aurata Chevrolat 1835: No. 162. Type material: LECTOTYPE (here selected) labelled: (illegible handwritten label); Chevrolat Carabidae Fr. V. d. Poll. Pres. 1909 E.B. Poulton; TYPE COL: 125 1/2 Catascopus aurata Chevr. HOPE DEPT. OXFORD [HECO]. Type locality: near Las Vigas, Veracruz, México.-- Chaudoir 1869: 180.

Description.-- Character states of the *C. aurata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Dorsum metallic green to dark brunneous with greenish luster; lateral margins of elytra slightly paler; appendages brunneous to rufo-piceous; antennae testaceous to brunneous;

mouthparts brunneous to piceous; terminal palpomeres with apices testaceous; labrum testaceous laterally toward base.

Elytra. Interneurs punctate.

Male genitalia. Median lobe as in Figs. 17C-17D, with apical portion medium-short, in lateral-left aspect trianguloid, slender, narrow, in dorsal aspect broader, and irregular in outline; apex in lateral aspect narrowly rounded, in dorsal aspect more broadly so.

Notes about habitat.-- Specimens were taken in Guatemala at altitudes of 243-914 m and in México at 30-1219 m. Specimens were taken under bark in Guatemala, Honduras, México, and Nicaragua; beating live and dead vegetation, at uv light and in a tropical riparian forest in México.

Geographical distribution (Map 5).-- This species ranges in Nuclear Middle America from México on the Gulf Versant north of the Isthmus of Tehuantepec, southward to Nicaragua.

Chorological affinities.-- The range of this species is separated widely from that of its adelphotaxon, *C. viridis*.

Phylogenetic relationships (Fig. 36).-- *Coptodera aurata* and *C. viridis* are postulated to be adelphotaxa, as shown by similarities in form of the median lobe of the male genitalia (Figs. 17C-17F).

Material examined.-- A total of 130 specimens, including types, were examined. Non-type material was seen from the following localities:

EL SALVADOR (USNM).

GUATEMALA Escuintla. El Zapote (MNHP); Finca El Zapote, Zapote (FMNH); Mirandilla (BMNH); Pantaleon (BMNH)(MNHP)(USNM); **Quezaltenango**. El Reposo (BMNH)(MCZ)(USNM); Las Mercedes (BMNH)(MNHP); **San Marcos**. El Zumbador (="El Tumbador") (AMNH)(BMNH); **Suchitepéquez**. Cuyotenango, Finca San Rafael Olimpo (CNC) Collections in February and July.

HONDURAS Comayagua. Taladro (UCBC). Collection in January.

MÉXICO (BMNH)(CUIC)(HNHM); **Chiapas**. Cd. Cuauhtemoc (UASM); 7.9 km n Frontera Comalapa (UASM); 7 km w Rizo de Oro (UASM); 18.3 km s Solosuchiapa, Rte. 195 (UASM); Tapachula (BMNH); **Oaxaca**. Temascal (CAS); 9 km s Valle Nacional, Rte. 175 (UASM); **Puebla**. Puente Tepexco, nr Tepexco, Rte. 115 (UASM); 24.1 km e Tezuitlan (CNC); **Veracruz**. Almolonga (BMNH); Bobo (AMNH)(BMNH)(MCZ)(MNHP); Cordova (BMNH); Cosamatoapam (BMNH); Fortin de las Flores (OSUC); Coyame, Lake Catemaco (UASM); Jalapa (AMNH)(BMNH)(MNHP); Lake Catemaco (UASM); Playa Vicente (BMNH)(MNHP); Rio Metlac, Fortin de las Flores (UCBC); Rio Metlac Canyon, 4 km s Fortin (CUIC); 4 km w Sontecomapan (UASM). Collections in April to August.

NICARAGUA Esteli. 8 km n Esteli (CAS)(CNC). Collections in July.

Coptodera viridis, new species
Figs. 17E & 17F; Map 5

Type material.-- HOLOTYPE, male labelled: MEX. Jalisco nr. Ixtapa gallery forest, dead tree.ca.100' XII.22.70; Puerto Vallarta, MEX. trip, 1970 G.E. and K.E. Ball collectors [USNM]. ALLOTYPE, female labelled same as holotype [USNM]. 16 additional PARATYPES, sex and label data as follows: 7 males and 6 females same as holotype [BMNH][CNC][MCZ][MNHP] [UASM]. 1 female: MEX. Jalisco 2 kil.s.e.Las Palmas,ca.400' thorn forest, dead log XII.26.70; Puerto Vallarta, MEX. trip, 1970 G.E. and K.E. Ball collectors [UASM]. 1 female: Maria Madre Id. village May. 14,1925; Tres Marias Islands; H.H.Keifer Collector [CAS]. 5 males and 2 females:

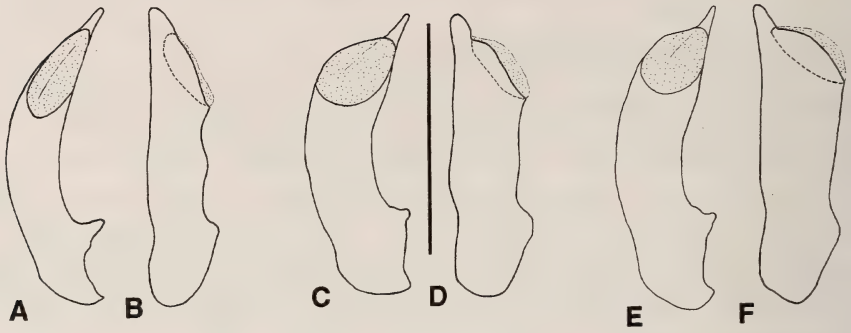
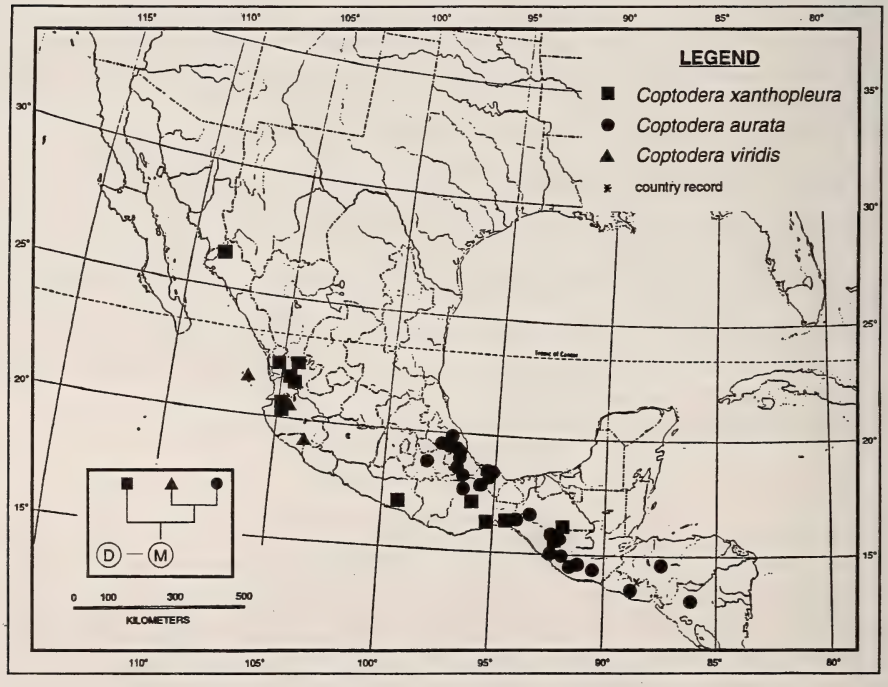


FIGURE 17. Line drawings of male genitalia of *Coptodera aurata* group. Figs. A, C & E left lateral aspect. Figs. B, D & F dorsal aspect. Figs. A-B: *C. xanthopleura* Bates. Figs. C-D: *C. aurata* Chevrolat. Figs. E-F: *C. viridis*, new species. Scale bars 1 mm.



MAP 5. Geographical distribution of *Coptodera xanthopleura* Bates, *C. aurata* Chevrolat and *C. viridis*, new species. Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

Maria Madre Id. village May 23,1925; Tres Marias Islands; H.H.Keifer Collector [CAS]. 1 female: MEXICO: 7 mi. NE. of Colima XII-3-1948; E.S. Ross Collector [CAS].

Type locality.-- Near Ixtapa, in the state of Colima, México.

Derivation of specific epithet.-- From the Latin adjective *viridis*, in allusion to the green color of this species.

Description.-- Character states of the *C. aurata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Dorsum metallic green to dark brunneous with greenish luster; lateral margins of elytra slightly paler; appendages brunneous; antennae and mouthparts dark testaceous to brunneous; palps with apices testaceous; labrum testaceous laterally towards base.

Elytra. Interneurs finely punctate.

Male genitalia. Median lobe as in Figs. 17E-17F; with apical portion short, in lateral-left aspect trianguloid, slender, narrow, in dorsal aspect trianguloid, broader; apex in left lateral aspect narrowly rounded, in dorsal aspect more broadly so.

Notes about habitat.-- This species has been taken at altitudes of 30-120 m; in gallery forest, thorn forest, from dead tree, and from a log.

Geographical distribution (Map 5).-- This species is known only from the Pacific Versant of southwestern México north of the Isthmus of Tehuantepec.

Chorological affinities and phylogenetic relationships (Fig. 36).-- See topics for *C. aurata* above, the adelphotaxon of *C. viridis*.

Material examined.-- Type material only; see above for details.

Coptodera depressa Group

This group has two species which are characterized by a notched anterior margin of the labrum which is slightly wider than long, four discal setigerous punctures in the third interval on each elytron, elytra with variegated color pattern to unicolorous, markedly developed upper spur on the inner surface of the fore-femur, and mid-tibia of male notched on ventral surface near apex. See Table I for features of mandibles. Male genitalia with median lobe pleuropic-left; membranous portion elongate; internal sac without macrotrichia or macrospines (Figs. 19A-19D). Ovipositor with ensiform setae of stylomere 2 dorsal (cf. Fig. 12I); nematiform setae present. The geographical range (Map 6) of this group is northern and central South America, including the Amazon Basin and the Southern Atlantic zone.

Chorological affinities.-- The range of this group (Map 6) is broadly overlapped by most other groups of New World *Coptodera*.

Phylogenetic relationships (Fig. 35).-- This group is the adelphotaxon of the other groups of the 4-punctate lineage (lineage R, Fig. 35).

Coptodera depressa Dejean
Figs. 18A-18C, 19A & 19B; Map 6

Coptodera depressa Dejean 1831: 393. Type material: LECTOTYPE male, labelled: TYPE (red paper); depressa Klug in Brasilia (green paper); D. Klug (green paper); undulata Perty Mait:5; Ex Musaeo Chaudoir (red print); depressa Dejean Brésil Coll Dejean (original box label);

Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: Brazil.-- Dejean & Boisduval 1829: 147.-- Chaudoir 1869: 166.

Coptodera undulata Perty 1830: 5, t. 1, f. 12. Type material: HOLOTYPE male, labelled: (green disc); Type.; undulata Perty (hand written); Holotypus Coptodera undulata Perty 1830 Zool. Staatssammlg. München (red paper) [ZSMM]. Type locality (here selected): Buenos Aires, state of Buenos Aires, Argentina.-- Chaudoir 1869: 166.

Coptodera plaumanni Liebke 1939: 127. NEW SYNONYMY. Type material: LECTOTYPE (here selected) male, labelled: (♂ on point supporting specimen); Chaco-Argentina Resistencia 2-1936- Col: M.VIANA (handwritten); Sammlung M. Liebke Hamburg; Kotype (pink paper); Coptodera plaumanni Lbk. M. Liebke determ. Kotype; Inst. Zool. P.A.N. Warszawa 31/54; Inst. Zool. P.A.N. Warszawa Cotypus Nr. 1351 (red paper) [IZWP]. Type locality: Resistencia, Argentina.

Notes about synonymy.-- The pale elytral markings of this species vary from markedly developed (Fig. 18A) to reduced (Figs. 18B & 18C) or completely lacking. Liebke based his description of *C. plaumanni* on six specimens which have reduced pale elytral markings. All these forms are conspecific. Based on examination of type material of the two named forms, we confirm the synonymy of *C. depressa* = *C. undulata*.

Description.-- Character states of the *C. depressa* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum rufo-piceous, moderately metallic green to aeneous; elytra rufo-piceous, with greenish, aeneous, or faint purpureous lustre and testaceous to rufo-testaceous markings or without pale markings (unicolorous); lateral margin of elytra rufo-testaceous; appendages, antennae, and mouthparts rufo-testaceous to rufo-brunneous. Ventral surface rufo-brunneous.

Elytra (Figs. 18A-18C). Interneurs finely punctulate to impunctate.

Legs. The fore-femur of the male lacks the dense brush of setae from the ventral surface as seen in *C. versicolor*.

Male genitalia. Median lobe as in Figs. 19A-19B, with apical portion in lateral-left aspect moderately long, trianguloid, tapered gradually to apex, in dorsal aspect with sides parallel; apical portion in line with sagittal plane of median lobe; apex in lateral-left aspect acute, almost pointed, in dorsal aspect broadly rounded.

Notes about variation.-- The pale elytral markings vary from markedly developed to completely lacking (Figs. 18A-18C).

Notes about habitat.-- Adults were taken on trees and logs at night and on a logpile at night in a forest in Argentina.

Geographical distribution (Map 6).-- The range of this species appears to be in southeastern and central South America including the Southern Atlantic zone and Amazon Basin, and probably along the northern coast of South America to Colombia.

Chorological affinities.-- The range of *C. depressa* probably overlaps that of *C. versicolor* in the western part of the Amazon Basin (Map 6).

Phylogenetic relationships (Fig. 36).-- This species is the postulated adelphotaxon of *C. versicolor*.

Material examined.-- A total of 182 specimens, including types, were examined. Non-type material was seen from the following localities:

ARGENTINA La Pampa (Pico) (MCZ); **Chaco**. Resitencia (IZWP). **Misiones** bords du Rio Iguazu, chutes de l'Iguazu (MNHP); Iguazu Nat. Park (CMNC); 20 km s.e., Iguazu (CMNC); Jardin America, Salto Tabay (CMNC). Collections were made in July and December to February.

BRAZIL (BMNH)(FMNH)(IZWP)(MCZ)(MNHP)(ZSMM); **Bahia**. (BMNH)(MNHP); **Espirito Santo**. Esp. Santo (HNHM); Espirito Santo (BMNH)(UASM); **Goiás**. (MNHP); Corumba, Fazenda Monjolinho (MZSP); Jatahy (MNHP); Rio Verde (MNHP); **Minas Gerais**. Mar de Hespanha (BMNH); **Parana**. Rondon (MCZ); **Rio de Janeiro** Rio Jan. (BMNH)(CMNH)(MNHP); **Rio Grande do Sul**. (MCZ)(MNHP); Rio Grande (BMNH); **Santa Catarina**. (MCZ)(MNHP); Corupa (Hansa Humboldt) (AMNH)(MCZ); Hansa Humboldt (MNHP); Nova Teutonia (AMNH) (CAS)(MCZ)(UASM)(USNM)(ZSMM); **São Paulo**. (MNHP); Cerqueira Cesar (MNHP); Rio Piracicaba (MNHP); São Paulo (BMNH)(IZWP); Val. du Rio Pardo (MNHP). Not located "Boa Sorta" (BMNH)(MNHP). Collections were made throughout the year.
COLOMBIA (BMNH).
PARAGUAY Alto Parana. Puerto P. Stroessner (HNHM); 27 km w Pto. Pres. Stroessner (EGRC); **Concepción**. vic. Horqueta (MCZ); **Itapúa**. Hohenau (UASM). Collections were made in January and June.
TRINIDAD (UASM). Collection in July.

Coptodera versicolor Bates
Figs. 2H, 8C, 8D, 18D, 19C & 19D; Map 6

Coptodera versicolor Bates 1869: 76. Type material: LECTOTYPE (here selected) female, labelled: Ega; versicolor Bates; affinis Chd; ex Musaeo H.W. Bates 1892 Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega (=Tefé), Amazonas, Brazil.
Coptodera affinis Chaudoir 1869: 168. Type material: LECTOTYPE (here selected) male, labelled: TYPE (red paper); affinis Chaud (handwritten); Ex Musaeo Chaudoir (red print); versicolor Bates Amazone Bates (original box label); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega (=Tefé), Amazonas, Brazil.-- Bates 1870: XVI.

Notes about type material.-- Chaudoir's description was based on "two female specimens from Ega". The Chaudoir material in the MNHP consisted of two specimens, a male and a female. We assume that Chaudoir must have misidentified the sex of one of the specimens.

Comparisons.-- Males of *C. sallei* also exhibit a dense brush of setae on the ventral surface of the fore-femur.

Description.-- Character states of the *C. depressa* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum rufo-piceous, moderately to brilliantly metallic green to aeneous; elytra rufo-piceous with greenish lustre basally and testaceous to rufo-testaceous markings, some specimens with overall aeneous lustre; lateral margin of elytra rufo-testaceous; appendages, antennae, and mouthparts testaceous to rufo-testaceous. Ventral surface rufo-brunneous.

Mouthparts. Left mandible as in Fig. 2H.

Elytra (Fig. 18D). Interneurs punctate.

Legs. Fore-femur of male with ventral brush of setae (Figs. 8C-8D).

Male genitalia. Median lobe as in Figs. 19C-19D, with apical portion flattened, in lateral-left aspect moderately long, trianguloid, tapered gradually to apex, in dorsal aspect trianguloid, gradually sloped to apex; apical portion slightly to right of sagittal plane of median lobe; apex in lateral-left aspect acute, almost pointed, in dorsal aspect broadly rounded.

Notes about habitat.-- Specimens were taken in the following countries at these altitudes: Bolivia at 400 m; Colombia at 213 m; Ecuador at 100 m; Peru at 290 m; and Venezuela at 140 m. Specimens were taken under bark of fresh cut tree in Ecuador; on logs, at uv light, and in

subtropical rainforest in Peru; and under bark of cut timber with bracket fungi in a rainforest in Venezuela.

Geographical distribution (Map 6).-- The range of this species is extensive in the Amazon Basin of cis-Andean South America.

Chorological affinities and phylogenetic relationships (Fig. 36).-- See these topics for *C. depressa* above, the adelphotaxon of *C. versicolor*.

Material examined.-- We examined 58 specimens, including types, and saw non-type material from the following localities:

BOLIVIA Cochabamba. (MNHP); Chaparé region (ZSMM); **Santa Cruz**. Valle Grande (MNHP). Collections were made in August to October, December, and February.

BRAZIL (MNHP); Amazon (BMNH); **Amazonas**. Ega (BMNH)(MNHP); Fonte Boa (MNHP); Sto. [sic] Paulo d'Olivença (MNHP); **Mato Grosso** Utiariti (MZSP); **Para**. (BMNH)(CMNH) (MNHP); Santarem (CMNH). Collections were made in June and July.

COLOMBIA Amazonas. Leticia (CNC)(UASM). Collection was made in July.

ECUADOR Napo Pastaza. Limoncocha (UASM); **Santiago-Zamora**. Macas (BMNH). Collection was made in April.

PERU Huallaga. (MNHP); Chambireyacu, nr. Yurimaguas (MNHP); Huánuco. Monzon Valley, Tingo Maria (CAS); **Loreto**. Rio Ampiyacu (FMNH); **Madre de Dios**. Manu National Park (CAS); Pakitza, 11°55'48"S 71°35'19"W (USNM); Pakitza, 12°07'S 70°58'W (USNM); Rio Tambopata Res., 30 km (air) sw Pto. Maldonato, 12°50'S69°20'W (BMNH)(USNM). Not located "**Loreto**. Cavallo-Cocho" (MNHP). Collections were made in May to December.

VENEZUELA Amazonas. Cerro de Neblina basecamp 0°50'N 66°10'W (USNM). Collection was made in February.

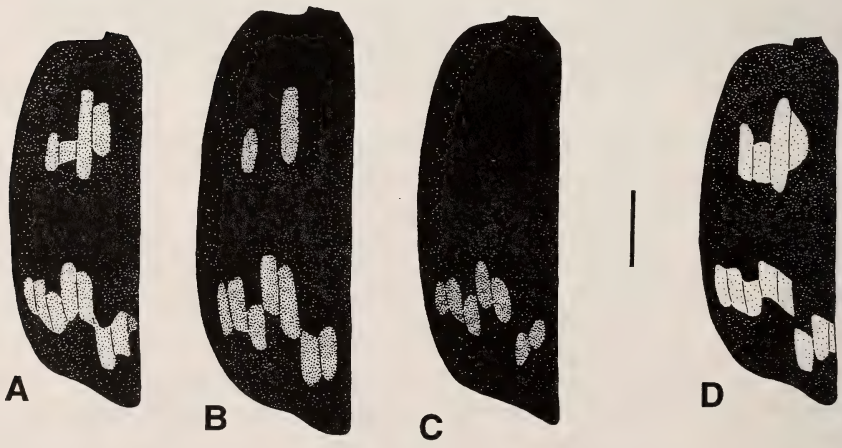


FIGURE 18. Line drawings of left elytron of *Coptodera depressa* group, dorsal aspect. Figs. A-C: *C. depressa* Dejean. Fig. D: *C. versicolor* Bates. Scale bars = 1 mm.

MAP 6. Geographical distribution of *Coptodera depressa* Dejean and *C. versicolor* Bates. Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

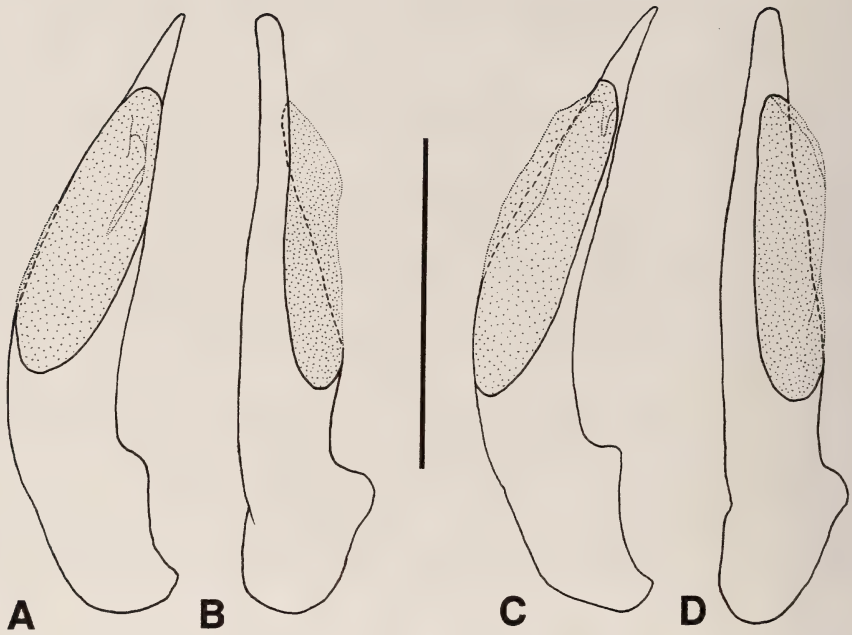


FIGURE 19. Line drawings of male genitalia of *Coptodera depressa* group. Figs. A & C left lateral aspect. Figs. B & D dorsal aspect. Figs. A-B: *C. depressa* Dejean. Figs. C-D: *C. versicolor* Bates. Scale bars = 1 mm.

Coptodera transversa Group

This group has nine species which are characterized by a shallowly emarginate anterior margin of labrum which is longer than wide, base of pronotum slightly to distinctly lobed medially, three or four discal setigerous punctures on each elytron, interneurs finely punctulate, elytra with variegated color pattern, markedly reduced or markedly developed upper spur on inner surface of the fore-tibia, and mid-tibia of male with notch on ventral surface near apex. See Table I for features of mandibles. Male genitalia with median lobe pleuropic-left; membranous portion short; internal sac without macrotrichia or macrospines (Figs. 21A-21P and 22A-22B). Ovipositor with ensiform setae of stylomere 2 dorsal (Fig. 12E); nematiform setae present. The geographical range of this group is extensive, from the Southern Atlantic zone of Brazil, through cis-Andean Colombia and north through Lower and Nuclear Central America to the Gulf and Pacific Versants of México north to the Isthmus of Tehuantepec.

Chorological affinities.-- The geographical range of the *C. transversa* group is broadly overlapped by most other groups of New World *Coptodera*.

Phylogenetic relationships (Fig. 36).-- This group is the postulated adelphotaxon of the *C. festiva* - *C. aerata* group lineage.

Coptodera dromioides (Bates), new combination
Figs. 20A, 21A & 21B; Map 7

Stenoglossa dromioides Bates 1869: 79. Type material: LECTOTYPE (here selected) female, labelled: Ega; dromioides Bates corticalis Chaud; ex Musaeo H.W. Bates 1892; LECTO TYPE (disc); LECTOTYPE Stenoglossa dromioides Bts det. George E. Ball 72 [MNHP]. Type locality: Ega, state of Amazonas, Brazil.

Stenoglossa corticalis Chaudoir 1869: 207. Type material: LECTOTYPE (here selected) male, labelled: Salhberg jun (hand written); corticalis Chaud (hand written); Brésil Cantagallo (hand written); Ex Musaeo Chaudoir (red print); LECTO TYPE (disc); LECTOTYPE Stenoglossa corticalis Chd det. George E. Ball 72 [MNHP]. Type locality: Cantagallo, state of Rio de Janeiro, Brazil.-- Bates 1870: XVII.

Recognition.-- This species is readily separated from other species of the *C. transversa* group on a combination of the following two characters: isodiametric elytral microsculpture and elytral color pattern.

Description.-- Character states of the *C. transversa* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head rufo-brunneous to brunneous; pronotum bicolored, rufo-brunneous to dark brunneous, with narrow testaceous anterior and posterior margins; elytra rufo-brunneous to nearly piceous with testaceous markings; appendages, antennae and mouthparts testaceous to brunneo-testaceous; ventral surface moderately to broadly testaceous along mid-line longitudinally, darkened to dark brunneous laterally, sternum 6 not pale medially; proepipleuron slightly paler or not; elytral epipleuron testaceous to brunneo-testaceous.

Fixed setae. Each elytron with four discal setae.

Elytra (Fig. 20A). Apical margin nearly straight; lateral margin hardly explanate in females.

Legs. Well developed upper spur on the inner surface of the fore-tibia.

Male genitalia. Median lobe as in Figs. 21A-21B, with apical portion in lateral-left aspect medium-short, rod-like, slightly tapered, in dorsal, aspect slender, rod-like with parallel sides; apex in lateral-left and dorsal aspects narrowly rounded.

Notes about habitat.-- Specimens were taken at 300-500 m in Brazil and at 840 m in Peru.

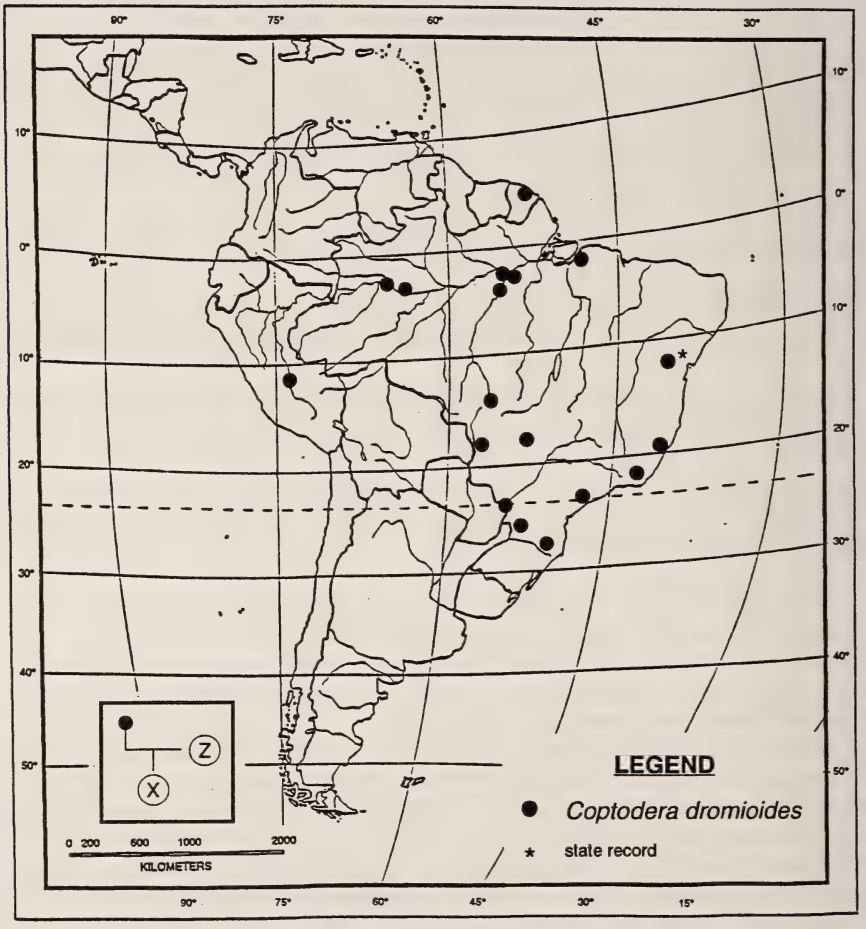
Geographical distribution (Map 7).-- This species is known only from Brazil (Southern Atlantic zone and Amazon Basin), French Guiana in northeastern South America, Paraguay, and cis-Andean Peru, to the west.

Chorological affinities.-- The geographical range of this species is overlapped broadly by the ranges of the other species in the *C. transversa* group (Maps 8-10).

Phylogenetic relationships.-- This species is the adelphotaxon of the remaining species in the *C. transversa* group.

Material examined.-- We examined 62 specimens, including types, and saw non-type material from the following localities:

BRAZIL Amazon (MNHP); **Amazonas** Ega (MNHP); Fonte Boa (MNHP); Itaituba (MNHP); Teffe (MNHP); **Bahia**. (MNHP); **Espirito Santo**. Esp. Santo (HNHM); **Goias**. Jatahy (MNHP); **Mato Grosso**. (MNHP); Chapada (CMNH); Corumba (CMNH); **Para**. (BMNH); Pará (MCSN); Santarem (BMNH)(CMNH); Tapajos (MNHP); **Rio de Janeiro** N. Friborg (MNHP); **Santa Catarina**. Nova Teutonia (USNM); São **Paulo**. Piracicaba (UASM); São Paulo (BMNH)(MNHP); Val du Rio Pardo (MNHP). Collections in October to December.
FRENCH GUIANA Cayenne (MNHP).
PARAGUAY Alto Parana. Puerto P. Stroessner (HNHM). Collection in December.
PERU Junín. Sani Beni, 8 km e Satipo (SEMC). Collection in November.



MAP 7. Geographical distribution of *Coptodera dromioides* (Bates). Inset indicates phylogenetic relationship of species as illustrated in Fig. 36.

Coptodera nigrosignata (Chaudoir), new combination
Figs. 20B, 21C & 21D; Map 8

Stenoglossa nigrosignata Chaudoir 1869: 206. Type material: LECTOTYPE (here selected) female, labelled: Ex Musaeo Chaudoir (red print); LECTO TYPE (disc); LECTOTYPE Stenoglossa nigrosignata Chd det. George E. Ball 72; fulminans Bates Amazone Ega Bates (handwritten box label); MUSEUM PARIS 1952 COLL R. OBERTHUR (light green paper) [MNHP]. Type locality: Ega, state of Amazonas, Brazil.

Recognition.-- This species is readily separated from other species of the *C. transversa* group on the combination of two characters: isodiametric elytral microsculpture and elytral color pattern.

Description.-- Character states of the *C. transversa* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum testaceous to brunneo-testaceous; elytra testaceous to brunneo-testaceous with rufo-brunneous to dark brunneous markings; appendages, antennae and mouthparts testaceous; ventral surface broadly testaceous along mid-line longitudinally, abdominal sterna darkened slightly laterally, sternum 6 with apical margin paler, remainder of ventral surface darkened to brunneous laterally; proepipleuron and elytral epipleuron testaceous to brunneo-testaceous.

Fixed setae. Each elytron with four discal setae.

Elytra (Fig. 20B). Apical margin nearly straight; lateral margin slight explanate in females.

Legs. Well developed upper spur on the inner surface of the fore-tibia.

Male genitalia. Median lobe as in Figs. 21C-21D, with apical portion in lateral-left aspect short, trianguloid, tapered gradually to apex, in dorsal aspect tapered gradually, abruptly widened at apex; apex in lateral-left aspect narrowly rounded, in dorsal aspect obliquely truncate.

Notes about habitat.-- None available.

Geographical distribution (Map 8).-- This species in known only from the Amazon Basin of Brazil.

Chorological affinities.-- The range of this species is isolated from that of the related *C. fulminans*, but is overlapped broadly by the range of another relative, *C. nigrostriata*.

Phylogenetic relationships (Fig. 36).-- This species is part of a trichotomy with *C. fulminans* and the *C. nigrostriata* - *C. stockwelli* lineage.

Material examined.-- We examined 12 specimens, including types, and saw non-type material from the following localities:
BRAZIL Amazonas. Fonteboa (MNHP); Maturacá, Rio Negro (MPEG); **Mato Grosso**. (MNHP); Sinop (CMNH); **Para**. (CMNH).Collections in October and January.

Coptodera fulminans (Bates), new combination
Figs. 20C, 21E & 21F; Map 8

Stenoglossa fulminans Bates 1869: 78. Type material: HOLOTYPE female, glued on card, labelled: fulminans Bates Bahia (hand written); nigrosignatus Chaud? (hand written); Ex Musaeo H.W. Bates 1892; HOLOTYPE Stenoglossa fulminans Bts det. George E. Ball 72 [MNHP]. Type area: state of Bahia, Brazil.
Stenoglossa nigrosignata: Bates 1870: XVII (not Chaudoir).

Note about synonymy.-- Bates (1870: XVII) misinterpreted Chaudoir's *C. nigrosignata*, as shown by study of type material.

Recognition.-- This species is readily separated from the other species of the *C. transversa* group on a combination of two characters: isodiametric elytral microsculpture and elytral color pattern.

Description.-- Character states of the *C. transversa* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum testaceous to brunneo-testaceous; elytra testaceous to brunneo-testaceous with rufo-brunneous to brunneous markings; appendages, antennae and mouthparts testaceous; ventral surface broadly testaceous along mid-line longitudinally, darkened to brunneous laterally, sternum 6 brunneo-testaceous to rufo-brunneous with apical margin paler; proepipleuron and elytral epipleuron testaceous.

Fixed setae. Each elytron with four discal setae.

Elytra (Fig. 20C). Apical margin nearly straight; lateral margin slightly explanate in females.

Legs. Well developed upper spur on the inner surface of the fore-tibia.

Male genitalia. Median lobe as in Figs. 21E-21F, with apical portion in lateral-left aspect medium-short, slender, tapered gradually, the parallel-sided, curved dorsally, in dorsal aspect sides gradually tapered to apex; apex in lateral-left and dorsal aspects narrowly rounded.

Notes about habitat.-- One specimen was taken at 30 m in Brazil.

Geographical distribution (Map 8).-- This species is known only from the Southern Atlantic zone of Brazil.

Chorological affinities.-- The geographical range of this species is isolated from the ranges of *C. nigrosignata*, *C. nigrostriata*, *C. lineata* and *C. stockwelli*.

Phylogenetic relationships (Fig. 36).-- See topic for *C. nigrosignata* above.

Material examined.-- We examined 4 specimens, including the type, and saw non-type material from the following localities:

BRAZIL Minas Gerais. Caraça (MNHP); **Paraiba**. Joao Pessoa, forest of Buranquinho (CMNH); **Santa Catarina**. Nova Teutonia (CAS). Collections in January and July.

Coptodera nigrostriata (Reiche), new combination
Figs. 10A, 20D, 21G & 21H; Map 9

Tetragonoderus nigrostriatus Reiche 1843: 179. Type material: HOLOTYPE female, labelled: Tetragonoderus nigrostriatus Reiche Venezuela (hand written); Ex Musaeo Chaudoir (red print); HOLOTYPE Stenoglossa nigrostriata Reiche det. George E. Ball 72 [MNHP]. Type locality: near Caracas, Venezuela.

Stenoglossa nigrostriata: Chaudoir 1869: 203.

Dromius multiguttata Putzeys 1845: 377. Type material: Not located. Type locality: Cumaná, state of Sucre, Venezuela.

Stenoglossa multiguttata: Chaudoir 1869: 203.

Stenoglossa variegata Chaudoir 1848: 117. Type material: HOLOTYPE labelled: variegata type Chaud (hand written); Ex Musaeo Chaudoir (red print); HOLOTYPE Stenoglossa variegata Chd det. George E. Ball 72 [MNHP]. Type area: Venezuela.-- Chaudoir 1869: 203.

Stenoglossa pallida Bates 1869: 78. Type material: LECTOTYPE (here selected) labelled: Ega (hand written); nigrostriata Reiche pallida Bates (hand written); H.W. Bates Biol Cent Amer;

MAP 8. Geographical distribution of *Coptodera nigrosignata* (Chaudoir) and *C. fulminans* (Bates). Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

LECTO TYPE (disc); LECTOTYPE Stenoglossa pallida Bts det. George E. Ball 72 [MNHP]. Type locality: Ega, state of Amazonas, Brazil.-- Bates 1870: XVII.

Notes about synonomy.-- We were unable to locate the type of *S. multiguttata* Putzeys. K. Desender (pers. comm.) also was unable to find the type specimen in the Institut Royal des Sciences Naturelles de Belgique in Brussels. We accept Chaudoir's synonymy of *S. multiguttata*. We confirm the status of the other junior synonyms on the basis of study of type material.

Recognition.-- This species is readily separated from other species in the *C. transversa* group on a combination of three characters and geographical distribution: isodiametric elytral microsculpture, markedly developed upper spur on the inner surface of the fore tibia, elytral color pattern, and known only from northern South America.

Description.-- Character states of the *C. transversa* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum testaceous to brunneo-testaceous; elytra testaceous to brunneo-testaceous with rufo-brunneous to brunneous markings; appendages, antennae and mouthparts testaceous to brunneo-testaceous; ventral surface broadly testaceous to brunneo-testaceous along mid-line longitudinally, darkened to brunneous laterally, sternum 6 brunneo-testaceous to rufo-brunneous with apical margin paler; proepipleuron and elytral epipleuron testaceous to brunneo-testaceous; sternum 6 not testaceous medially.

Fixed setae. Each elytron with four discal setae.

Elytra (Fig. 20D). Apical margin sinuate; lateral margin markedly explanate in females.

Legs. Well developed upper spur on the inner surface of the fore-tibia.

Abdominal sterna. Sterna III-V of male as in Fig. 10A.

Male genitalia. Median lobe as in Figs. 21G-21H, with apical portion in lateral-left aspect short, trianguloid, tapered gradually to apex, in dorsal aspect sides gradually tapered to apex; apex in lateral-left and dorsal aspects narrowly rounded.

Notes about habitat.-- Specimens were taken at 609 m in Colombia and at 200 m in Peru. Specimens were taken by beating during the day in a primary forest in Brazil and on logs, under bark and from a cornstone polypore in Peru.

Geographical distribution (Map 9).-- This species is known only from the Amazon Basin and northward in cis-Andean South America.

Chorological affinities.-- The range of this species is adjacent to, but is not known to overlap the range of its adelphotaxon, *C. lineata* + *C. stockwelli.*

Phylogenetic relationships.-- This species is the adelphotaxon of the species pair *C. lineata* + *C. stockwelli.*

Material examined.-- We examined 31 specimens, including types, and saw non-type material from the following localities:

BOLIVIA Cochabamba. (MNHP).

BRAZIL Amazon (MNHP); **Amazonas**. Ega (MCSN)(MNHP); 30 km w Itaquatiara, Rio Urubu (CMNH); *Mato Grosso.* (MNHP); Chapada (CMNH). Collections in November and January.

COLOMBIA Magdelena. Don Amo (CMNH). Collection in July.

COLOMBIA/PEROU (MNHP).

PERU Madre de Dios. 15 km ne Puerto Maldonado (SEMC). Collections in July.

VENEZUELA (MNHP).

Coptodera lineata (Bates), new combination
Figs. 20E, 21I, 21J, 22A & 22B; Map 9

Stenoglossa lineata Bates 1883: 184. Type material: LECTOTYPE (here selected) male, labelled: Type H.T. (disc with red border); Chacoj Vera Paz Champion; Stenoglossa lineata Bates; Stenoglossa lineata Bates (hand written); LECTOTYPE ♂ Stenoglossa lineata Bts By Erwin '76 [BMNH]. Type locality: Chacoj, state of Alta Verapaz, Guatemala.-- Ball 1975: 172.

Recognition.-- This species is readily separated from other species of the *C. transversa* group on a combination of two characters: isodiametric elytral microsculpture and elytral color pattern.

Description.-- Character states of the *C. transversa* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head testaceous to brunneo-testaceous; pronotum testaceous; elytra testaceous with rufo-brunneous to nearly piceous markings; appendages, antennae and mouthparts testaceous; ventral surface moderately to broadly testaceous along mid-line longitudinally, darkened to nearly piceous laterally, sternum 6 rufo-brunneous to dark brunneous with apical margin paler; proepipleuron and elytral epipleuron testaceous.

Fixed setae. Each elytron with four discal setae.

Elytra (Fig. 20E). Apical margin shallowly sinuate; lateral margin markedly explanate in females.

Legs. Well developed upper spur on inner surface of fore-tibia.

Male genitalia. Median lobe as in Figs. 21I, 21J, 22A-22B, with apical portion in lateral-left aspect very short, rectangular, in dorsal aspect trianguloid, acutely tapered; apex in lateral-left aspect broadly rounded, in dorsal aspect narrowly rounded.

Notes about habitat.-- Specimens were taken in the following countries at these altitudes: Guatemala, 731 m; México, 30-122 m; and Panamá, 243-457 m. Specimens were taken under bark, on wilted leaves and dry wood at night in Costa Rica; under bark, on logs, on dead tree in a gallery forest, on a dead log in a thorn forest, and in a rain forest in México.

Geographical distribution (Map 9).-- This range of this species extends from western Panamá northward to the Gulf and Pacific Versants of México north of the Isthmus of Tehuantepec.

Chorological affinities.-- The ranges of this species and its adelphotaxon, *C. stockwelli*, overlap in Chiriqui Province, western Panamá.

Phylogenetic relationships (Fig. 36).-- This species is the adelphotaxon of *C. stockwelli.*

Material examined.-- We examined 140 specimens, including types, and saw non-type material from the following localities:

COSTA RICA Limón. Hamburg Farm (BMNH)(USNM). Collections in February, March, May, June, August, and October.

GUATEMALA Alta Verapaz. Chacoj (BMNH); **Escuintla** Finca El Zapote, Zapote (FMNH); Pantaleon (BMNH); Zapote (BMNH)(MNHP). **Quezaltenango** Las Mercedes (BMNH); El Reposa (BMNH). Collection in July.

MÉXICO Chiapas. San Quintin (UASM); **Jalisco**. nr. Ixtapa (UASM); El Limon (UCBC); 2 km s e Las Palmas (UASM); **Quintana Roo**. 17 km nw Felipe Carrillo Puerto (RHTC); **San Luis Potosí**. Tamazunchale (CAS); **Tabasco**. La Chontalpa (USNM); **Veracruz**. Almolonga (BMNH)(USNM); Cerro de Plumas (BMNH)(MNHP); Lake Catemaco (UASM); 4 km w Sontecomapan (UASM); 25.7 km n w Tuxpan (CAS). Collections in February, April, June and December.

NICARAGUA Chontales. (BMNH).

PANAMA Chiriqui. Bugaba (BMNH)(MCZ)(USNM); 2 km n Sta. Clara, Hartmann's Finca 08°51'N 82°36'W (CNC) **Panamá**. Pozo Azul, Finca Vega near Las Nubes (CAS). Collection in April.

Coptodera stockwelli, n. sp.
Figs. 7B, 20F, 21K & 21L; Map 9

Type material.-- HOLOTYPE male, labelled: ♂ +wing; ADP 25397; PANAMA. C.Z. Madden Forest 9°06'N-79°36'W 1.2mi. E cont.div. 30 June 1974; T.L.Erwin, D.R. Whitehead Colls. running on under- side of log; Expedition #28 in notebook #3 [USNM]. ALLOTYPE female, labelled same as holotype except: ♀ +wing; ADP 25414 [USNM]. 118 PARATYPES, sex and label data as follows: 16 males same as holotype except: ADP 25398.....ADP 25413 (different number on each specimen) [BMNH][CAS][CNC][MCZ][UASM][USNM]. 1 male same as holotype except: ♀ +wing; ADP 25415 [USNM]. 1 male same as holotype except: ADP 25416 [USNM]. 10 males same as holotype except: ADP 25387.....ADP 25396 (different number on each specimen) [USNM]. 7 males same as holotype except: ADP 25994.....ADP 2600 (different number on each specimen) [USNM]. 1 female same as allotype except: ADP 25414 [USNM]. 14 females same as allotype except: ADP 25417.....ADP25430 (different number on each specimen) [BMNH][CAS][CNC][MCZ][UASM][USNM]. 1 female same as allotype except: ♂ +wing; ADP 25999 [USNM]. 2 females same as allotype except: ADP 26001 and ADP 26002 (different number on each specimen) [USNM]. 1 male and 2 females: Panamá: Canal Zone Madden Forest, Mi. 2.5 9°05'N 79°37'W 28 Jun.'72 G.Otis; running on log; ADP 47485 (male) ADP 47466 and ADP 47487 (one for each female respectively); Stenoglossa sp. (male only); [HPSC]. 3 males and 2 females: Panamá: Canal Zone Madden Forest, Mi. 2.5 9°05'N 79°37'W 13 July '74 Stockwell; running on underside of elevated log; ADP 46029, ADP 46052, ADP 46054 (one for each male respectively), ADP 460515 and ADP 46050 (one for each female respectively) [USNM]. 2 males and 3 females: PANAMA, dist. Chepo Altos de Maje 17 May 75 at lights Stockwell - Engleman; ADP 44945 and ADP 44967 (one for each male respectively), ADP 44940, ADP 44942, and ADP 44944 (one for each female respectively) [HPSC]. 1 female: PANAMA, dist. Chepo Altos de Maje 17 May 75 at lights Stockwell - Engleman [DHK]. 1 male: ♂ +winged; ADP 42864; PANAMA:Canal Zone Achiote Rd 0046 M 010.0 mi SW Gatum 0912N 07956W; under bark 01 Mar 1975 04-044 T.L.Erwin & J.L.Lawrence [USNM]. 1 male: ADP 83267; PANAMA: Canal Zone Barro Colorado Is. 10 April 1977; H. Wolda Project Light Traps Nivel SMI [USNM]. 1 male: Barro Colorado I. Canal Zone, PANAMA Jan. 17-19 1959; CNHM Panama Zool. Exped. (1959) H.S. Dybas leg.; ♂ +wing; ADP 08174 [FMNH]. 2 males and 1 female: ♀ +wing; ADP 27331 and ADP 27332 (males) and ADP 27333 (female); CANAL ZONE,Madden Forest VII-3-1974 O'Briens&Marshall [USNM]. 1 male: Paraiso CZ PanApr1411 EASchwarz; ♂ +wing; ADP 08180 [USNM]. 4 females: PANAMA:Canal Zone; Barro Colorado I. I:22:1959 leg. H.S. Dybas [FMNH]. 1 male: TrinidadRiv Pan. 1.VI.12 AugustBusck; ♂ +wing; ADP 08185 [USNM]. 2 females: Tabernilla CanalZone Panama; May 17.07; Aug. Busck Collector; ♀ +wing; ADP 08155 and ADP 08184 (one for each female respectively) [USNM]. 1 female: Alhajuelo CZ Pan; 27 May 1912; A Busck coll; ♀ +wing; ADP 08183 [USNM]. 1 female: CabimaPan May 22 11 AugustBusck; ♂ +wing; ADP 18181 [USNM]. 1 male: V. de Chiriqui 2-3000 ft. Champion; Ex Godman and Salvin; Stenoglossa nigrostriata Bates (handwritten); ♀ +wing; ADP 08154 and ADP 08156 (one for each male respectively); sten 1 (yellow paper; on first male); HOMOTYPE (red type) Stenoglossa nigrostriata R. (handwritten; on first male) [MCZ]. 4 males: V. de Chiriqui, 2-3000 ft. Champion; H.W.Bates Biol.Cent.Amer.; Museum Paris ex Coll.R. Oberthur (light green paper); Stenogl. sp. 8 Shpeley & Ball det. G.E. Ball '90 [MNHP]. 1 male and 1 female (on a single pin): Ciricito Canal Zone 2/25/30 (green paper); 11008 (green paper); 11009 (green paper); Blackwelder Collection (blue paper); ♂ +wing; ♀ +wing; ADP 08189; ADP 80190 [USNM]. 2 females (on a single pin): Ciricito Canal Zone

2/25/30 (green paper); 11010 (green paper); 11011 (green paper); Blackwelder Collection (blue paper); ♀ +wing (two labels); ADP 08187; ADP 08188 [USNM]. 1 female: CiricitoCZ Mar 20 1930 Blackwelder (blue paper); Blackwelder Collection (blue paper); ♀ +wing; ADP 08186; sten 2 (yellow paper); HOMOTYPE (red type) Stenoglossa lineata Bts (handwritten); HOMOTYPE (red type) Stenoglossa nigrosignata Chd. (handwritten); HOMOTYPE (red type); Stenoglossa variegata Chd. (handwritten) [USNM]. 1 male: PANAMA: Bayano Dist. 2 km. W Ipeti 22 May 1991 R. Turnbow [RHTC]. 1 male: PANAMA: Panama Prov. 11-15 km. N El Llano 24 May 1991 R. Turnbow [RHTC].

Type locality.-- Madden Forest, Canal Zone, Panamá.

Derivation of specific epithet.-- Latinized surname of Dr. Henry P. Stockwell, renowned coleopterist of the Panamá Canal Zone, who collected several of the type specimens.

Recognition.-- This species is readily separated from other species of the *C. transversa* group on a combination of three characters and geographical distribution: isodiametric elytral microsculpture, markedly developed upper spur on the inner surface of the fore-tibia, elytral color pattern and known only from Panamá.

Description.-- Character states of the *C. transversa* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head testaceous to nearly rufo-testaceous; pronotum testaceous; elytra testaceous with rufo-brunneous to nearly piceous markings; appendages, antennae and mouthparts testaceous; ventral surface broadly testaceous along mid-line longitudinally, darkened to brunneous laterally, sternum 6 brunneo-testaceous to rufo-testaceous with apical margin paler; proepipleuron and elytral epipleuron testaceous.

Fixed setae. Each elytron with four discal setae.

Pronotum. As in Fig. 7B.

Elytra (Fig. 20F). Apical margin sinuate; lateral margin markedly explanate in females.

Legs. Well developed upper spur on the inner surface of the fore-tibia.

Male genitalia. Median lobe as in Figs. 21K-21L, with apical portion in lateral-left aspect very short, rectangular, in dorsal aspect with sides nearly parallel; apex in lateral-left aspect broadly rounded, in dorsal aspect narrowly rounded.

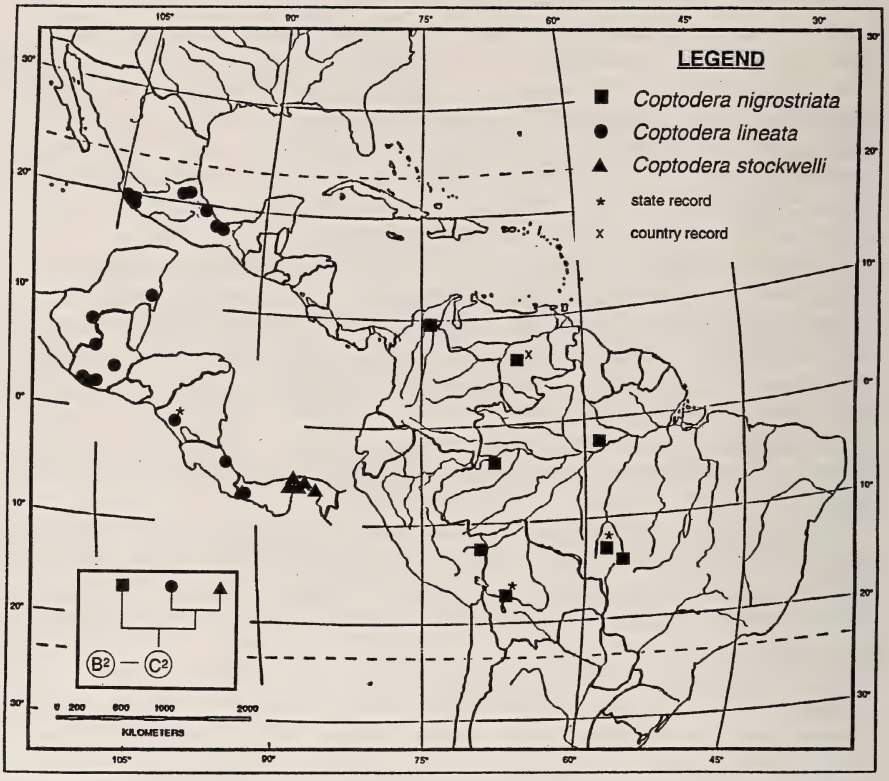
Notes about variation.-- Six specimens (1 MCZ, 4 MNHP, and 1 USNM) collected at Volcan Chiriqui have a bicolored pronotum, but the male genitalia are identical to those of other specimens of this species. The central area of the elytral disc is pale, with a longitudinal rufo-brunneous marking on each side before the pale lateral margin.

Notes about habitat.-- Specimens were taken at 46-914 m in Panamá at light, on logs, on cut wood at night, and under bark.

Geographical distribution (Map 9).-- This species is known only from Panamá, in Lower Central America.

Chorological affinities and phylogenetic relationships (Fig. 36).-- See these topics for *C. lineata* above, the adelphotaxon of *C. stockwelli.*

Material examined.-- Type material only, see above for details.



MAP 9. Geographical distribution of *Coptodera nigrostriata* (Reiche), *C. lineata* (Bates) and *C. stockwelli*, new species. Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

Coptodera transversa (Reiche), new combination
Figs. 3A-3F, 10B, 12E-12H, 20G, 21M & 21N; Map 10

Tetragonoderus transversus Reiche 1843: 179. Type material: LECTOTYPE (here selected) male, labelled: Tetragonoderus (hand written); transversus Reiche Rev. Cuvier 1843; Ex Musaeo Chaudoir (red print) [MNHP]. Type area: Colombia.

Stenoglossa transversa: Chaudoir 1869:204.

Stenoglossa atriceps Bates 1869: 78. Type material: LECTOTYPE (here selected) male, labelled: Ega (hand written); transversa Reiche atriceps Bates (hand written); H.W. Bates Biol. Cent. Amer.; LECTO TYPE (disc); LECTOTYPE Stenoglossa atriceps Bts det. George E. Ball 72 [MNHP]. Type locality: Ega, state of Amazonas, Brazil.-- Bates 1870: XVII.

Stenoglossa picturata Chaudoir 1869: 205. NEW SYNONOMY. Type material: LECTOTYPE (here selected) male, labelled: picturata Chaudoir Amerique Sallé; Ex Musaeo Chaudoir (red

print); LECTO TYPE (disc); LECTOTYPE Stenoglossa picturata Chd det. George E. Ball 72 [MNHP]. Type area: México.

Stenoglossa undulata Chaudoir 1869: 206. NEW SYNONOMY. Type material: LECTOTYPE (here selected) female, labelled: undulata Chaud Brésil Nov Frib. Squires (hand written); Squires; Ex Musaeo Chaudoir (red print); LECTO TYPE (disc); LECTOTYPE Stenoglossa undulata Chd det. George E. Ball 72 [MNHP]. Type locality: Nova Friburgo, state of Rio de Janeiro, Brazil.

Notes about synonomy.-- The type specimens associated with the junior synonyms recorded above do not differ significantly from the type specimen of *C. transversa* Reiche.

Recognition.-- This species is readily separated from other species in the *C. transversa* group on a combination of two characters: transverse elytral microsculpture and markedly reduced upper spur on the inner surface of the fore-tibia.

Description.-- Character states of the *C. transversa* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head brunneous to piceous; pronotum bicolored, disc dark testaceous to nearly piceous, anterior and lateral margins testaceous to nearly piceous, posterior margin testaceous; elytra testaceous with brunneo-testaceous to piceous markings; appendages and antennae dark testaceous to nearly brunneous; mouthparts brunneo-testaceous to dark brunneous; femora dark brunneous in basal two third; ventral surface rufo-testaceous to nearly piceous, sternum 6 with apical margin paler; elytral epipleuron testaceous.

Fixed setae. Each elytron with three discal setae.

Mouthparts. Mandibles as in Figs. 3A-3F.

Elytra (Fig. 20G). Apical margin sinuate; lateral margin markedly explanate in females.

Legs. Markedly reduced upper spur on the inner surface of the fore-tibia.

Abdominal sterna. Sterna III-V of male as in Fig. 10B.

Male genitalia. Median lobe as in Figs. 21M-21N, with apical portion in lateral-left aspect very short, quadrate, hardly tapered to apex, in dorsal aspect with sides slightly tapered; apex in lateral-left aspect broadly rounded, in dorsal aspect narrowly rounded.

Ovipositor. Stylomere 2 as in Figs. 12E-12H.

Notes about habitat.-- Specimens were taken in the following countries at these altitudes: Brazil, 100-500 m; Costa Rica, 1380-1390 m; Guatemala, 1400-2100 m; México, 30 to 2164 m; and Panamá, 1219-1524 m. Specimens were taken on tree trunks in Costa Rica; under bark and at u-v light in Guatemala; in a cloud forest, under bark, on logs and on bark of a recently fallen tree in México and in a light trap in Panamá.

Geographical distribution (Map 10).-- The range of this species extends from the Southern Atlantic zone of Eastern Brazil to cis-Andean Bolivia and Paraguay, and northward through the Amazon Basin and Lower and Nuclear Central America to the Pacific and Gulf Versants of México north of the Isthmus of Tehuantepec.

Chorological affinities.-- The range of this species overlaps the range of its adelphotaxon, *C. sigillata* + *C. squiresi.*

Phylogenetic relationships (Fig. 36).-- This species is the postulated adelphotaxon of the species pair *C. sigillata* + *C. squiresi.*

Material examined.-- We examined 280 specimens, including types, and saw non-type material from the following localities:

BOLIVIA Cochabamba. (MNHP).
BRAZIL Amazons (MNHP); **Amazonas**. Ega (MNHP); 30 km w Itaquatiara, Rio Urubu (CMNH); Manaus, 1 km w w Taruma Falls (CMNH); **Goias**. Jatahy (MNHP); Rio verde (MNHP); **Rio de Janeiro** Nov. Frib. (MNHP); Rio Jan. (MNHP); **Santa Catarina**. Nova Teutonia (BMNH)(CAS)(UASM)(USNM); **São Paulo**. (BMNH). Collections in all months of the year except February.
COLOMBIA.(MNHP).
COSTA RICA Limón. Hamburg Farm (USNM); **Puntarenas**. Monteverde (USNM); Monteverde, road to electric plant (USNM). Collections in June and August.
GUATEMALA Sacatepéquez. Finca San Rafael (FMNH); **Zacapa**. Sierra del Espiritu Santo, 3 km se La Union (UASM). Collections made in June.
MÉXICO Chiapas. 9.8 km n Ocosingo (RHTC); **Oaxaca**. Oaxaca (BMNH); **Queretero**. 8.3 km w San Luis Potosí Queretero border, Hwy. 120 (SEMC); **San Luis Potosí**. 29 km sw Tamazunchale (UCBC); **Veracruz**. Almolonga (BMNH)(MNHP); Cerro de Plumas (MNHP); 7 km n Huatusco (UASM); Jacale (BMNH); Jalapa (BMNH)(MNHP); 4 km w Sontecomapan (UASM). Collections in April and June to August.
PANAMA Canal Zone. Barro Colorado (USNM); **Chiriqui**. Boquete 08°48'N 82°26'W (USNM); Boquete 08°47'N 82°26'W (USNM); Bugaba (BMNH)(MNHP); Fortuna 08°44'N 82°15'N (USNM); Hartmann's Finca, 2 km n Sta. Clara 08°51'N 82°36'W (CNC); (USNM); Ojo de Agua, 4 km n Sta. Clara (USNM); V. de Chiriqui (BMNH)(MNHP); **Panamá**. Cerro Campana, Nr. Chica (USNM). Collections in April to June.
PARAGUAY Alto Paraná. Puerto P. Stroessner (HNHM). Collection in January.

Coptodera sigillata, n. sp.
Figs. 20H, 21O & 21P; Map 10

Type material.-- HOLOTYPE male, labelled: BRAZIL,Santa Cata- rina,Nova Teutonia II - 1977 Fritz Plaumann Cal.Acad.Sci.Coll. [CAS].

Type locality.-- Nova Teutonia, state of Santa Catarina, Brazil.

Derivation of specific epithet.-- From Latin *signum*, in allusion to the markedly defined dark markings on the elytra.

Recognition.-- This species is readily separated from the other species of the *C. transversa* group on a combination of three characters: transverse elytral microsculpture, markedly developed upper spur on the inner surface of the fore-tibia, and rounded sutural angle of the elytron.

Description.-- Character states of the *C. transversa* group and the following. See Tables II, IV and VI for data about standardized body length, and ratios Hw/Pw and Pw/Pl.

Color. Head rufo-brunneous; pronotum bicolored, disc rufo-brunneous, broad testaceous lateral margins, narrower testaceous anterior and posterior margins; elytra testaceous with dark brunneous to piceous markings; appendages, antennae and mouthparts testaceous to slightly darker; ventral surface broadly testaceous along mid-line longitudinally, darkened to dark brunneous laterally, sternum 6 rufo-brunneous with apical margin paler; proepipleuron and elytral epipleuron testaceous.

Fixed setae. Each elytron with three discal setae.

Elytra (Fig. 20H). Apical margin sinuate.

Legs. Well developed upper spur on the inner surface of the fore-tibia.

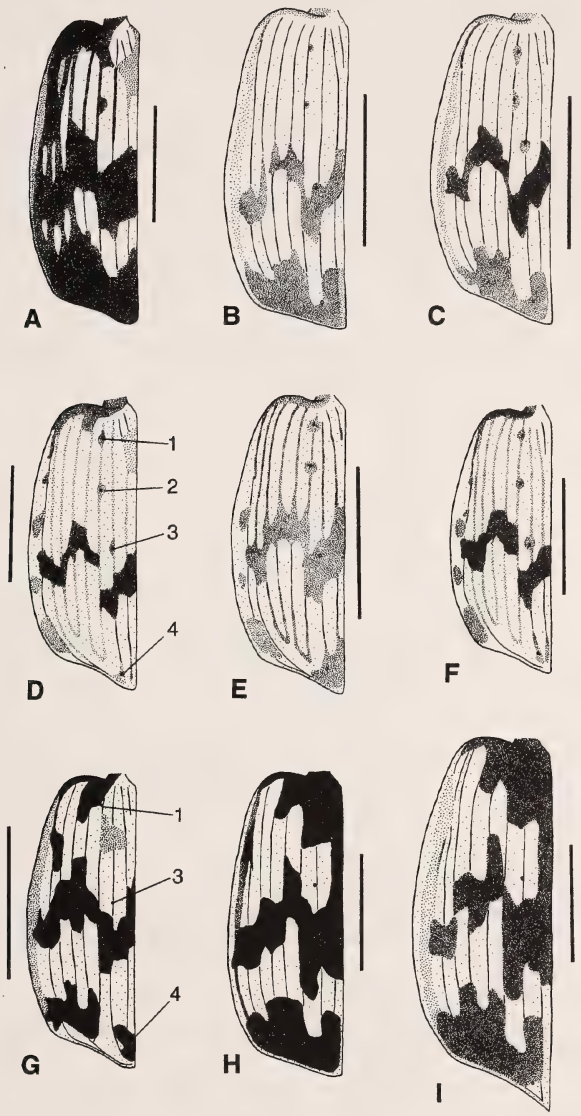


FIGURE 20. Line drawings of left elytron of *Coptodera transversa* group, dorsal aspect. Fig. A: *C. dromioides* (Bates). Fig. B: *C. nigrosignata* (Chaudoir). Fig. C: *C. fulminans* (Bates). Fig. D: *C. nigrostriata* (Reiche). Fig. E: *C. lineata* (Bates). Fig. F: *C. stockwelli*, new species. Fig. G: *C. transversa* (Reiche). Fig. H: *C. sigillata*, new species. Fig. I: *C. squiresi* (Chaudoir). Scale bars = 1 mm. Legend: 1, discal setigerous puncture #1; 2, discal setigerous puncture #2; 3, discal setigerous puncture #3; 4, discal setigerous puncture #4.

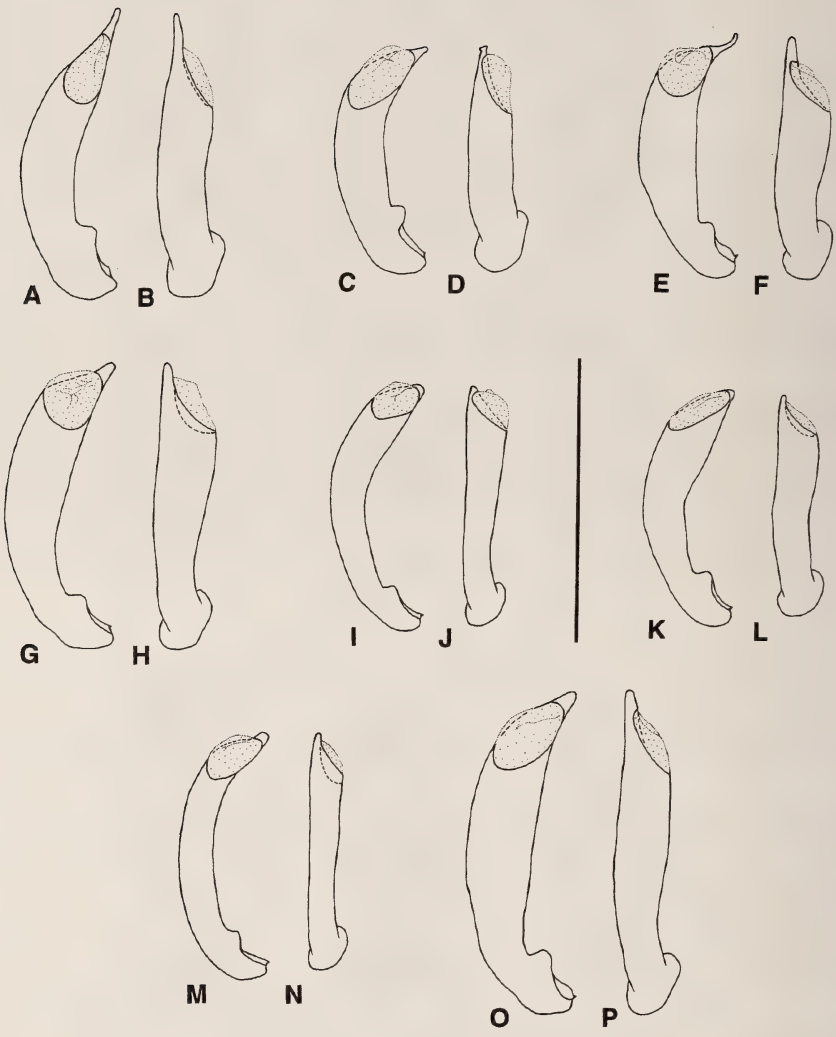


FIGURE 21. Line drawings of male genitalia of *Coptodera transversa* group. Figs. A, C, E, G, I, K, M & O left lateral aspect. Figs. B, D, F, H, J, L, N & P dorsal aspect. Figs. A-B: *C. dromioides* (Bates). Figs. C-D: *C. nigrosignata* (Chaudoir). Figs. E-F: *C. fulminans* (Bates). Figs. G-H: *C. nigrostriata* (Reiche). Figs. I-J: *C. lineata* (Bates). Figs. K-L: *C. stockwelli*, new species. Figs. M-N: *C. transversa* (Reiche). Figs. O-P: *C. sigillata*, new species. Scale bars = 1 mm.

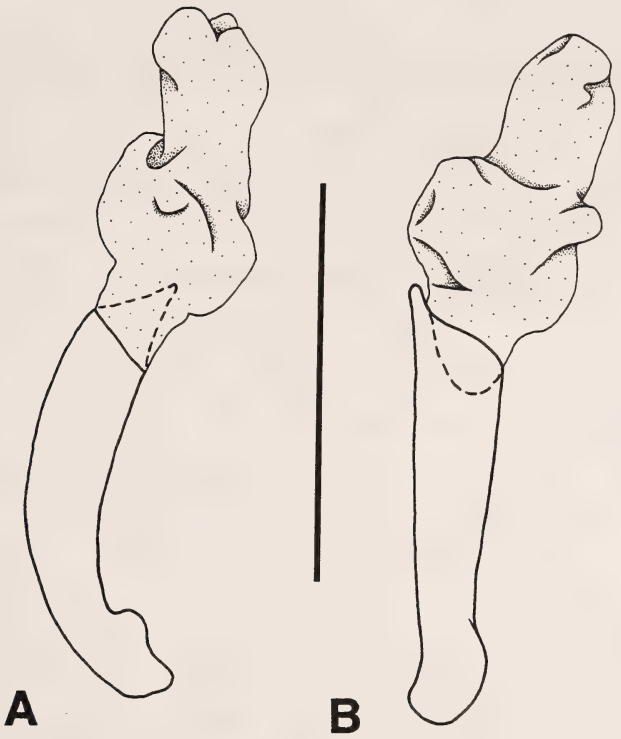


FIGURE 22. Line drawings of male genitalia of *C. lineata* (Bates). Figs. A & B left lateral and dorsal aspects respectively. Scale bars = 1 mm.

Male genitalia. Median lobe as in Figs. 21O-21P, with apical portion in lateral-left aspect very short, trianguloid, tapered gradually to apex, in dorsal aspect nearly parallel, hardly tapered; apex in lateral-left and dorsal aspects narrowly rounded.

Notes about habitat.-- None available.

Geographical distribution (Map 10).-- This species is known only from the type locality of Nova Teutonia, Santa Catarina, Brazil.

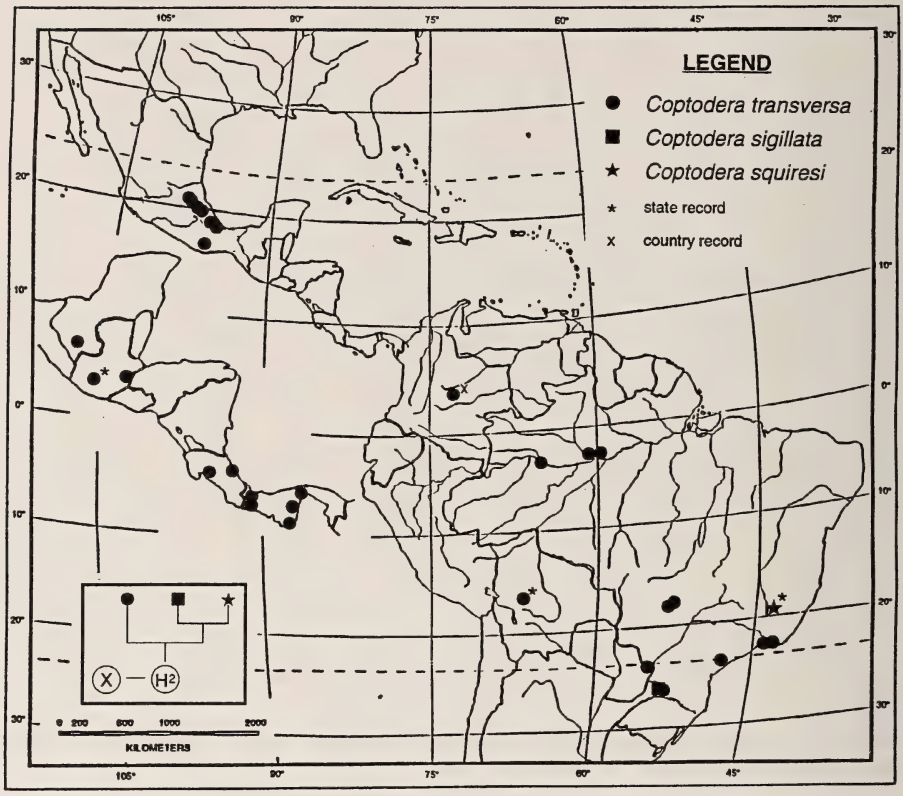
Chorological affinities.-- Both *C. sigillata* and its adelphotaxon are known from the Southern Atlantic zone of Eastern Brazil, but from different localities therein.

Phylogenetic relationships (Fig. 36).-- This species is the postulated adelphotaxon of *C. squiresi*.

Material examined.-- Holotype only, see above for details.

Coptodera squiresi (Chaudoir), new combination
Fig. 20I; Map 10

Stenoglossa squiresi Chaudoir 1869: 201. Type Material: LECTOTYPE female, labelled: Ex Musaeo Chaudoir (red ink); HOLO (red paper); TYPE (red paper); Squiresii Chaud. Brésil



MAP 10. Geographical distribution of *Coptodera transversa* (Reiche), *C. sigillata*, new species and *C. squiresi* (Chaudoir). Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

Minas Squires (hand written); MUSEUM PARIS 1962 COLL. R. OBERTHUR; HOLOTYPE Stenoglossa squiresi Chd det. George E. Ball 72 [MNHP]. Type area: State of Minas Gerais, Brazil.

Recognition.-- This species is readily separated from the other species of the *C. transversa* group by the acute sutural angle of the elytron.

Description.-- Character states of the *C. transversa* group and the following. See Tables III, V, and VII for data about standardized body length, and ratios Hw/Pw and Pw/Pl.

Color. Head rufo-brunneous; pronotum bicolored, disc rufo-brunneous, broad testaceous lateral margins, narrower testaceous anterior and posterior margins; elytra testaceous with rufo-brunneous markings; appendages, antennae and mouthparts testaceous; tibiae slightly darkened medially; ventral surface of pronotum, sterna medially and elytral epipleuron testaceous, remainder of ventral surface dark testaceous to brunneous; sternum 6 not testaceous medially.

Fixed setae. Each elytron with three discal setae.

Elytra (Fig. 20I). Sutural angle acute; apical margin sinuate; lateral margin moderately explanate in female.

Legs. Well developed upper spur on inner surface of fore-tibia.

Male genitalia. Male unknown.

Notes about habitat.-- None available.

Geographical distribution (Map 10).-- This species is only known from the type area of Minas Gerais in Brazil.

Chorological affinities and phylogenetic relationships.-- See these topics for *C. sigillata* above, the postulated adelphotaxon of *C. squiresi.*

Material examined.-- Holotype only, see above for details.

Coptodera festiva Group

This group has nine species which are characterized by a shallowly emarginate anterior margin of the labrum that is wider than long, four discal setigerous punctures on each elytron, elytra with a variegated color pattern, markedly developed upper spur on the inner surface of the fore-tibia, and mid-tibia of male with notch on the ventral surface near apex. See Table I for features of mandibles. Male genitalia with median lobe pleuropic-left; membranous portion various degrees of "medium"; internal sac with macrospines (Figs. 24A-24P). Ovipositor with ensiform setae of stylomere 2 on dorsal margin (cf. Fig. 12I); nematiform setae present. The geographical range of this group extends from the Southern Atlantic zone of Brazil northward through the Amazon Basin of cis-Andean South America, Lower and Nuclear Central America to México north of the Isthmus of Tehuantepec, the Greater Antilles and Southern Florida.

Chorological affinities.-- The geographical range of the *C. festiva* group is broadly overlapped by the combined ranges of its adelphotaxa, the *C. bifasciata*, *C. emarginata*, *C. picea* and *C. aerata* groups (Maps 11-20).

Phylogenetic relationships (Fig. 35).-- The *C. festiva* group is the adelphotaxon of the *C. bifasciata* - *C. aerata* group lineage.

Coptodera sahlbergi Chaudoir
Figs. 7C, 23A, 24A & 24B; Map 11

Coptodera sahlbergi Chaudoir 1869: 181. Type material: HOLOTYPE female, labelled: Ex Musaeo Chaudoir (red print); TYPE (red paper); Sahlbergi Chaud. Brésil Petropolis Sahlb. jun. (original box label); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Petropolis, Rio de Janeiro, Brazil.

Coptodera discicollis Chaudoir 1869: 181. NEW SYNONYMY. Type material: HOLOTYPE female, labelled: Bolivie (handwritten on light green paper); Ex Musaeo Chaudoir (red print); Discicollis Chaud. Bolivie Deyrolle (original box label); Museum Paris ex Coll R. Oberthür light green paper) [MNHP]. Type area: Bolivia.

Notes about synonymy.-- Chaudoir's two species names were based on two specimens which we believe to be conspecific. The specimen of *C. sahlbergi* shows reduced pale markings on the elytra, while *C. discicollis* has extensive pale markings. In all other regards, the two specimens are identical.

Description.-- Character states of the *C. festiva* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head rufo-brunneous to dark brunneous; pronotum rufo-brunneous to rufo-piceous with broad testaceous lateral margins; elytra brunneous to rufo-piceous, with testaceous markings; lateral margin of elytra testaceous; appendages, antennae, and mouthparts testaceous to brunneo-testaceous, tibiae and apices of femora darkened. Dorsal surface with greenish to aeneous lustre. Ventral surface testaceous except proepisternum, mesepisternum, mesepimeron, metasternum (laterally), metepisternum, and epipleuron at shoulder brunneo-testaceous to brunneous.

Pronotum. As in Fig. 7C.

Elytra (Fig. 23A). Interneurs finely punctulate.

Male genitalia. As in Figs. 24A-24B, median lobe with membranous portion medium-long; apical portion medium-short, in lateral aspect triangular, tapered gradually toward apex, in dorsal aspect rod-like, sides parallel; apex in lateral aspect narrowly rounded, in dorsal aspect sub-truncate. Internal sac spine A long; spine group B absent; spine group C with two long spines.

Notes about habitat.-- Specimens were taken in Brazil at altitudes of 300-700 m; in Paraguay at night.

Geographical distribution (Map 11).-- The known range of this species in South America extends from the southern edge of the Amazon Basin southward to northern Argentina and eastward to the Southern Atlantic zone.

Chorological affinities.-- The range of this species is allopatric to the ranges of most species in the *C. festiva* group, being overlapped by the most distantly related species pair, only (*C. rufescens* + *teutonica*, Map 12).

Phylogenetic relationships (Fig. 36).-- This species is the adelphotaxon of the remaining species in the *C. festiva* group.

Material examined.-- We examined 54 specimens, including types, and saw non-type material from the following localities:

ARGENTINA Tucumán. Tucumán (BMNH). Collection was made in October.

BRAZIL (HNHM); Amazon (MCZ); **Espirito Santo**. Espirito Santo (UASM); **Mato Grosso**. Chapada (=Chapada dos Guimaraes (CMNH); R. Caraguata (MCZ); **Minas Gerais**. Aguas Vermelhas (CMNH); **Parana**. Rolandia (AMNH)(MCZ); **Rio de Janeiro**. Itatiaya (BMNH); Lagune de Sacuaresma (MNHP); Rio de Jan. (CMNH); **Santa Catarina**. Nova Teutonia (CAS)(IZWP)(MCZ)(ZSMM); **São Paulo**. Barueri (MCZ)(MZSP); Campos Fordao (USNM); Faz. Itaquerê, Nova Europa (MZSP); Faz. Pau d'Alho Itú (MZSP); S. Paulo (HNHM); Val. du Rio Pardo (MNHP). Collections were made in September to April.

PARAGUAY Amambay. (MCZ); **Parahuarí**. Parc. Nac. Ybycuí (JKOC). Collection was made in January.

One specimen from the MCZ labelled "Santiago". One specimen from MNHP with a handwritten label that appears to be "Cuba", and if our interpretation is correct, then the specimen must be mislabelled.

Coptodera relucens Bates
Figs. 23B, 23C, 24C & 24D; Map 11

Coptodera relucens Bates 1869: 73. Type material: LECTOTYPE (here selected) male, labelled: LECTO (red paper); TYPE (red paper); (green rectangle); Ex Musaeo Chaudoir (red print); relucens Bates Amazone Ega Bates (original box label); Coptodera relucens Bates det. G.E.

Ball '87; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega, Amazonas, Brazil.

Coptodera lebioides Bates 1869: 74. NEW SYNONYMY. Type material: LECTOTYPE (here selected) male, labelled: Ega (handwritten); TYPE (red paper); Ex Musaeo H.W. Bates 1892; Lebioides Bates (handwritten); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega, Amazonas, Brazil.

Coptodera rotundipennis Chaudoir 1869: 182. Type material: LECTOTYPE (here selected) male, labelled: rotundipennis Chaud (handwritten); Ex Musaeo Chaudoir (red print); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega, Amazonas, Brazil.-- Bates 1870: XVI.

Note about synonymy.-- After examining the types of *C. relucens* and *C. lebioides*, we believe the two to be conspecific.

Description.-- Character states of the *C. festiva* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head rufo-testaceous to rufous, darkened medially or not; pronotum brunneo-testaceous to rufous, with aeneous lustre, with one longitudinal rufo-piceous marking each side of median line, lateral margin diffusely paler or not; elytra rufous to rufo-piceous, with aeneous lustre, and testaceous or dirty white markings; lateral margin of elytra testaceous; appendages, antennae, and mouthparts testaceous, tibiae and tarsomeres darkened. Ventral surface testaceous to rufo-testaceous.

Elytra (Figs. 23B-23C). Interneurs punctate.

Male genitalia. As in Figs. 24C-24D, median lobe with membranous portion medium-long; apical portion medium-long, in lateral aspect slender, spiculate, tapered apically, in dorsal aspect slender, sides parallel; apex in lateral aspect pointed, in dorsal aspect narrowly rounded. Internal sac spine A medium in length; spine group B with two long spines; spine group C with one long spine.

Notes about variation.-- This species exhibits two elytral color patterns, but the male genitalia are identical, indicating that both forms must be conspecific.

Notes about habitat.-- None available.

Geographical distribution (Map 11).-- This species is known only from the Amazon Basin, in Brazil.

Chorological affinities.-- This species and its adelphotaxon, *C. poecila*, are allopatric.

Phylogenetic relationships (Fig. 36).-- This species is the postulated adelphotaxon of *C. poecila*.

Material examined.-- We examined 8 specimens, including types, and saw non-type material from the following localities:

BRAZIL Amazonas. Ega (BMNH)(MNHP); **Mato Grosso**. Chapada (=Chapada dos Guimares (CMNH); **Para**. Santarem (CMNH). Not located "Chimboanga" (MNHP).

Coptodera poecila Bates
Figs. 23D, 24E & 24F; Map 11

Coptodera poecila Bates 1883: 183. Type material: HOLOTYPE male, labelled: Type HT (disc bordered with red); V. de Chiriqui 25-4000 ft. Champion; B.C.A. Col. I.1 Coptodera poecila, Bates; Coptodera poecila Bates (Bates' handwriting); HOLOTYPE ♂ Coptodera poecila Bates by Erwin '76 [BMNH]. Type locality: Volcan de Chiriqui, Chiriqui Prov., Panamá.

Description.-- Character states of the *C. festiva* group and the following. See Tables II, IV and VI for data about standardized body length, and ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum testaceous; elytra rufo-piceous with testaceous markings; antennae testaceous, antennomeres 2-4 darkened; mouthparts rufo-testaceous to rufo-brunneous (apical half of terminal palpomeres testaceous); femora testaceous, darkened apically; tibiae and tarsi dark brunneous. Dorsally, dark areas of elytra with faint green lustre. Ventral surface testaceous; metepisternum and metasternum rufo-testaceous; epipleuron rufo-piceous.

Elytra (Fig. 23D). Interneurs finely punctate.

Male genitalia. As in Figs. 24E-24F, median lobe with membranous portion medium-short; apical portion medium-long, in lateral aspect slender, tapered apically, in dorsal aspect slender, sides parallel; apex in lateral aspect pointed, in dorsal aspect narrowly rounded. Internal sac spine A medium in length; spine group B with two long spines; spine group C with two medium-short spines.

Notes about habitat.-- None available.

Geographical distribution (Map 11).-- This species is known only from the type locality, in Lower Middle America.

Chorological affinities.-- The type locality of this species is overlapped by the range of *C. festiva*, but it is separated from the range of its adelphotaxon, *C. relucens*.

Phylogenetic relationships (Fig. 36).-- See this topic for *C. relucens* above, the adelphotaxon of *C. poecila*.

Material examined.-- Holotype only.

Coptodera pakitza, new species
Fig. 23E; Map 11

Type material.-- HOLOTYPE, female labelled: PERU: MADRE DE DIOS Pakitza T.L.Erwin 29-Oct - 01Nov90 12°07'S 70°58'W; Forest type #12, on trunks along trail at Tr. Tachigali /42; BIOLAT/COLE 000008389 [USNM]. One female PARATYPE labelled same as holotype except third label is as follows: BIOLAT/COLE 000008385 [USNM].

Type locality.-- Pakitza, department of Madre de Dios, Peru.

Derivation of specific epithet.-- From "Pakitza", the name of the type locality.

Description.-- Character states of the *C. festiva* group and the following. See Tables III, V and VII for data about standardized body length, and ratios Hw/Pw and Pw/Pl.

Color. Head dark testaceous; pronotum bicolored, rufo-piceous macula surrounded with markedly broad testaceous lateral margins, anterior and posterior margins testaceous also; elytra dark brunneous to rufo-piceous with testaceous markings; lateral margin of elytron testaceous; appendages, antennae and mouthparts testaceous. Dark markings of dorsal surface with moderate green lustre, pale areas of elytra with faint green lustre. Ventral surface testaceous, abdominal sterna darkened laterally, thoracic sterna brunneo-testaceous to dark brunneous (elytral epipleuron testaceous).

Elytra (Fig. 23E). Interneurs finely punctate.

Male genitalia. Unknown.

Notes about habitat.-- Both specimens were taken on tree trunks along a forest trail.

Geographical distribution (Map 11).-- This species is known only from the type locality in southern cis-Andean Peru, in the upper reaches of the Amazon Basin.

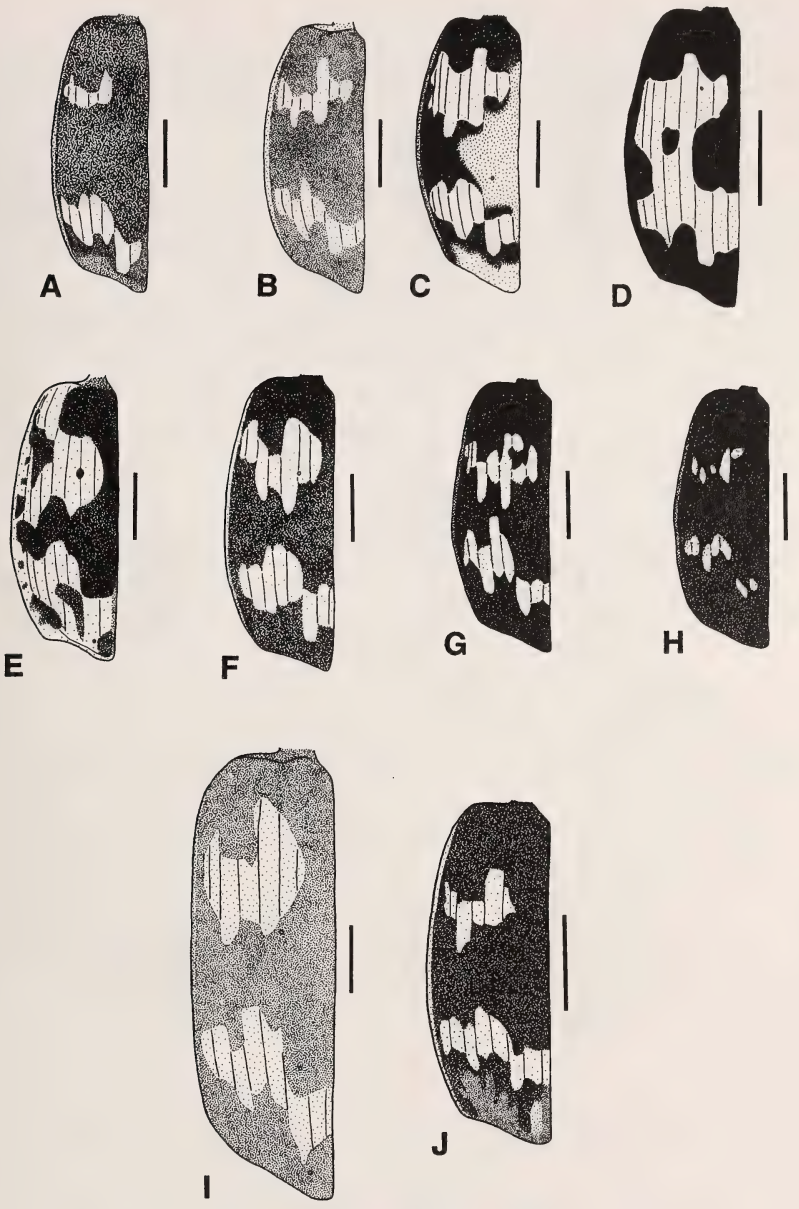


FIGURE 23. Line drawings of left elytron of *Coptodera festiva* group, dorsal aspect. Fig. A: *C. sahlbergi* Chaudoir. Figs. B-C: *C. relucens* Bates. Fig. D: *C. poecila* Bates. Fig. E: *C. pakitza* new species. Fig. F: *C. festiva* Dejean. Fig. G. *C. foveolata*, new species. Fig. H: *C. nigroviridis*, new species. Fig. I: *C. rufescens* Buquet. Fig. J: *C. teutonica*, new species. Scale bars = 1 mm.

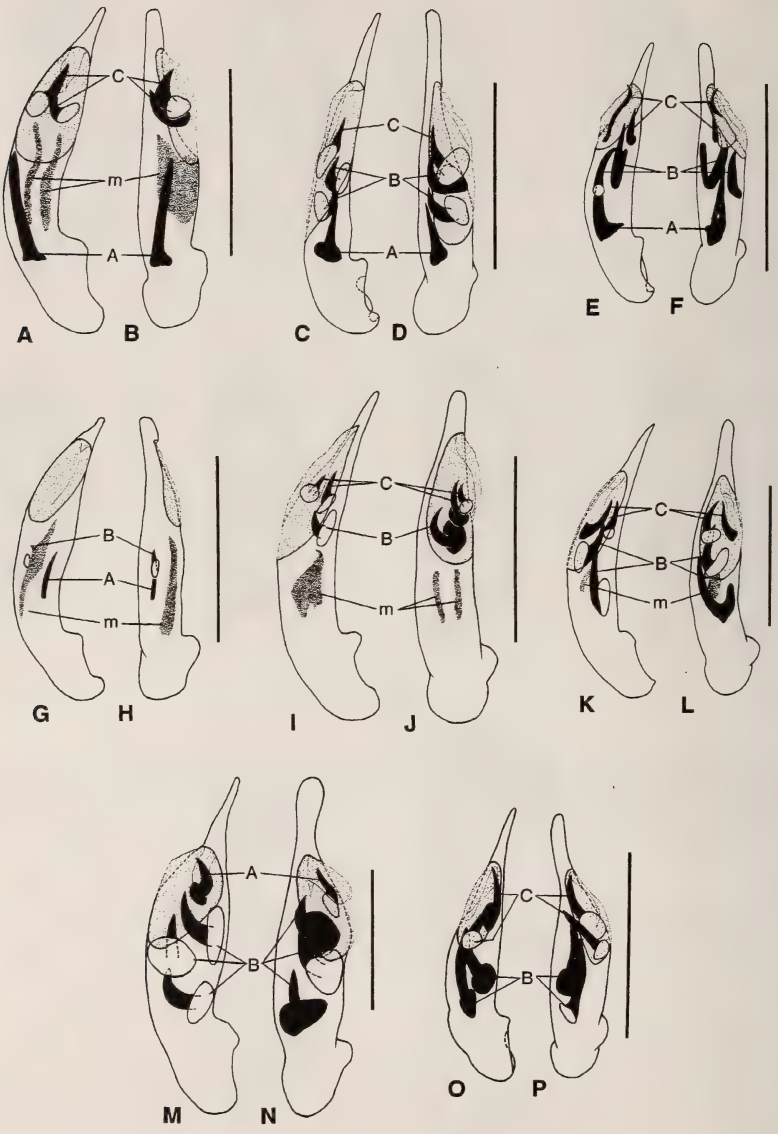
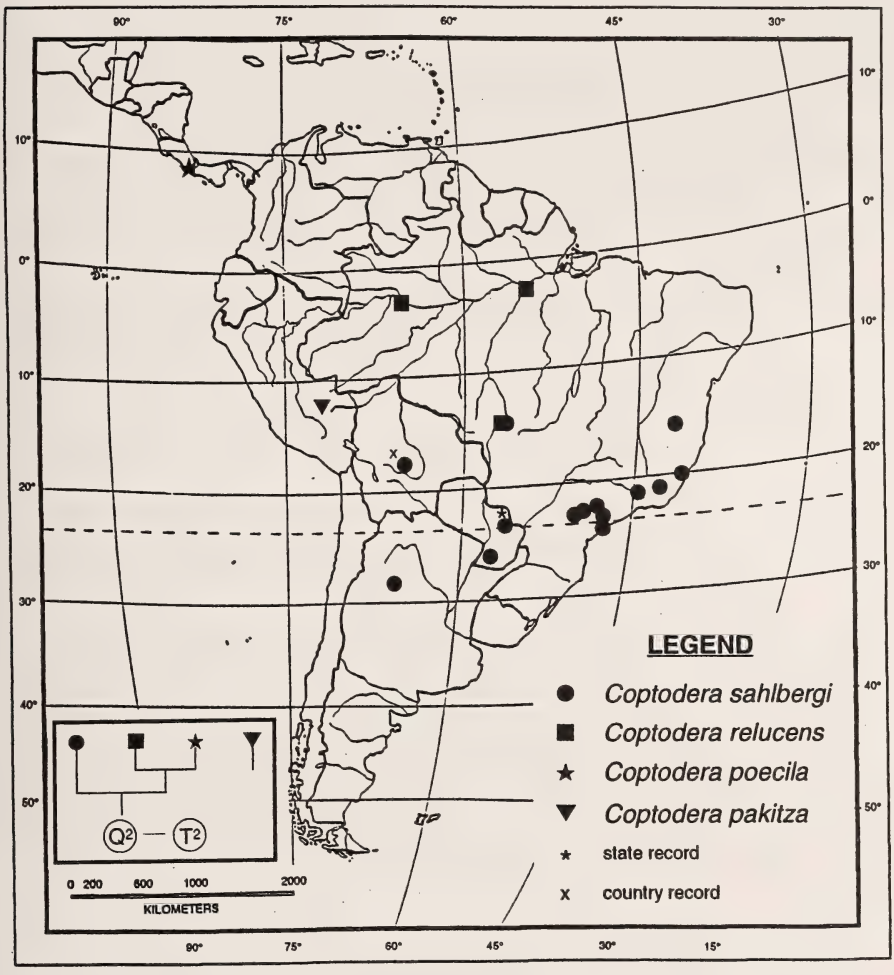


FIGURE 24. Line drawings of male genitalia of *Coptodera festiva* group. Figs. A, C, E, G, I, K, M & O left lateral aspect. Figs. B, D, F, H, J, L, N & P dorsal aspect. Figs. A-B: *C. sahlbergi* Chaudoir. Figs. C-D: *C. relucens* Bates. Figs. E-F: *C. poecila* Bates. Figs. G-H: *C. festiva* Dejean. Figs. I-J. *C. foveolata*, new species. Figs. K-L: *C. nigroviridis*, new species. Figs. M-N: *C. rufescens* Buquet. Figs. O-P: *C. teutonica*, new species. Scale bars = 1 mm. Legend: A, spine A; B, spine B; C, spine C; m, microtrichial field.



MAP 11. Geographical distribution of *Coptodera sahlbergi* Chaudoir, *C. relucens* Bates, *C. poecila* Bates and *C. pakitza*, new species. Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

Chorological affinities.-- The ranges of the other species in the *C. festiva* group do not overlap that of *C. pakitza*.

Phylogenetic relationships (Fig. 36).-- The position of this species is unresolved due to the lack of a male specimen; it is placed tentatively next to the *C. relucens* - *C. poecila* and *C. festiva* - *C. teutonica* lineages.

Material examined.-- Type material only, see above for details.

Coptodera festiva Dejean
Figs. 1E, 3G-3L, 23F, 24G & 24H; Map 12

Coptodera festiva Dejean 1825: 274. Type material: LECTOTYPE male, labelled: festiva mihi in ins. Cuba (Dejean handwriting on green paper); D. Ericher (Dejean handwriting on green paper); Ex Musaeo Chaudoir (red print); TYPE (red paper); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: Cuba.-- Chaudoir 1869: 182.-- Erwin & Sims 1984: 446.

Coptodera chloris Bates 1883: 182. NEW SYNONYMY. Type material: LECTOTYPE (here selected) male, labelled: Type H.T. (disc with red border); Mirador Mexico Hoege; B.C.A. Col. I.1 Coptodera chloris, Bates; Coptodera chloris Bates (handwritten [Bates']); LECTOTYPE ♂ Coptodera chloris Bates by Erwin '76 [BMNH]. Type locality: Mirador, Veracruz, México.

Notes about type material.-- In the BMNH are two additional male specimens, labelled: Mirador Mexico Hoege; B.C.A. Col. I.1 *Coptodera chloris*, Bates; and are here selected as PARALECTOTYPES. In the MNHP are two female specimens labelled: Mirador Mexico Hoege; H.W. Bates Biol Cent Amer; Museum Paris ex Coll R. Oberthür (light green paper); and are here selected as PARALECTOTYPES (one of the two specimens also bears a "TYPE" label on red paper).

Notes about synonymy.-- The type specimens of *C. festiva* and *Coptodera chloris* Bates are identical, and we believe them to be conspecific.

Description.-- Character states of the *C. festiva* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head testaceous to darkened medially; pronotum testaceous to brunneo-testaceous with disc slightly to broadly darkened each side of the mid-line; elytra brunneous to rufo-piceous, faint greenish to aeneous lustre (best observed basally), with testaceous markings; lateral margin of elytra testaceous; appendages, antennae, and mouthparts testaceous to rufo-testaceous. Ventral surface testaceous with epipleuron at shoulder brunneo-testaceous to brunneous (see notes on variation).

Mouthparts. Labrum as in Fig. 1E; mandibles as in Figs. 3G-3L.

Elytra (Fig. 23F). Interneurs impunctate.

Male genitalia. As in Figs. 24G-24H, median lobe with membranous portion medium-short; apical portion short, in lateral aspect trianguloid, tapered irregularly, rather bulbous, in dorsal aspect broader, sides about parallel; apex in lateral aspect narrowly rounded, in dorsal aspect more broadly rounded. Internal sac spine A short; spine group B with one short spine; spine group C absent.

Notes about habitat.-- In Costa Rica, specimens were taken at altitudes of 200-300 m. In Cuba, specimens were taken at altitudes of 182-914 m; in a wood pile. In Haiti specimens were taken at an altitude of 305 m. In México specimens were taken at altitudes of 30-1295 m; at rotting lemons; at mercury vapor and u-v light; in tropical seasonal forest; in tropical lowland forest. In Panamá specimens were taken at light; in glass fruitfly traps. Specimens were taken in blacklight traps in Puerto Rico. The single specimen from Florida was taken in a Malaise/flight intercept trap in a pineland forest.

Geographical distribution (Map 12).-- This species ranges through Lower and Nuclear Central America to both the Gulf and Pacific Versants of México, between the Tropic of Cancer and the Isthmus of Tehuantepec, and eastward to the Greater Antillean islands of Puerto Rico, Hispaniola, Jamaica and Cuba, and northward to the southern tip of Florida. The isolated occurrence of this species near Belém, Brazil, might be the result of an accidental importation there through shipping.

Chorological affinities.-- The range of this species overlaps those of *C. poecila*, *C. foveolata*, and *C. cupreotincta* in Middle America.

Phylogenetic relationships (Fig. 36).-- This species is the postulated adelphotaxon of the *C. foveolata* - *C. teutonica* lineage.

Material examined.-- A total of 127 specimens, including types, were examined. Non-type material was seen from the following localities:

BRAZIL Para. Belem (USNM)(ZSMM); Bôa, Vista Mu. Castanhal (USNM). Collections in October and January.

COSTA RICA Guanacaste. 3 km n Canas, Itac. La Pacifica (UASM); 4 km nw Canas, La Pacifica (CNC); **Limón**. Las Mercedes (USNM). Collections in April and June.

CUBA Las Villas. Soledad (Cienfuegos) (MCZ); Trinidad Mts. (MCZ)(MNHP); **Oriente**. Gran Piedra Rge. (MCZ); Rio Frio, Boniato Rge. (BMNH)(MCZ). Collections in May, June, and October.

GUATEMALA Petén. Tikal (FSCA). Collection in July.

HAITI Artibonite. Ennery (BMNH)(MCZ). Collection in August.

JAMAICA Surrey. St. Andrew. 136 Barbican Road (street address in Kingston)(JAMU); Irish Town (JAMU)(MCZ); St. Thomas. Bath (FSCA). Collections in July and October.

MÉXICO (IZWP); **Campeche**. Chicana ruins, 9.7 km e Xpujil (UASM); **Chiapas**. Chorreadera St. Pk. (LSUC); 1.4 km n Frontera Comalapa (UASM); Bonampak Rd., 100 km se Palenque (UASM); **Nayarit**. 37 km se Tepic (UASM); **Oaxaca**. 0.8 km e Tapanatepec, Rte. 190 (UASM); 10.5 km s Valle Nacional (UASM); **San Luis Potosí**. El Salto Falls, 12 km nw El Naranjo (SEMC); **Veracruz**. 33 km ne Catemaco, Los Tuxtla Biol. Stn. (UASM); Los Tuxtlas Biol. Stn., ca. 32.2 km e Catemaco (UASM); Los Tuxtla Biol. Station (UASM); Mirador (BMNH); Tebanca (UASM). Collections in May to August.

PANAMA (ZSMM); **Canal Zone**. Barro Colorado Is. (USNM); Panamá. El Cermeno (USNM); La Campana (USMN); Las Cumbres (OSUC); Taboga Island (BMNH). Collections in April to July, and September to December.

PUERTO RICO Rd. 10, Km. 24 (JMPR). Collections in June and September.

UNITED STATES Florida. Dade Co. Camp Mahachee, nr. Matheson Hammock (FSCA); Everglades N.P., Long Pine Key (SPC). Collections were made in July to September and December.

Coptodera foveolata, new species
Figs. 23G, 24I & 24J; Map 12

Type material.-- HOLOTYPE male, labelled: MEXICO. Vera Cruz Tebanca. ex. foliage, fallen tree. 27.vi.1985 Askevold & Heffern [USNM]. ALLOTYPE female, labelled same as holotype [USNM]. 1 male PARATYPE, labelled same as holotype [UASM].

Type locality.-- Tebanca, state of Veracruz, México.

Derivation of specific epithet.-- From Latin *fovea*, in allusion to the large setigerous foveae on the disc of each elytron.

Description.-- Character states of the *C. festiva* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head brunneous; pronotum rufo-brunneous to brunneous with broad testaceous lateral margins; elytra brunneous to rufo-piceous with testaceous markings; lateral margin of elytra testaceous to rufo-testaceous; appendages, antennae, and mouthparts brunneo-testaceous to rufo-testaceous, tibiae and tarsomeres darkened. Dorsal surface with moderate green lustre. Ventral surface testaceous with thoracic sterna brunneo-testaceous to brunneous (epipleuron not darkened at shoulder).

Elytra (Figs. 23G). Discal setae set in foveate punctures; interneurs finely punctate.

Male genitalia. As in Figs. 24I-24J, median lobe with membranous portion medium-long; apical portion medium-short, in lateral aspect slender, rod-like, hardly tapered, in dorsal aspect broader; apex in lateral aspect narrowly rounded, in dorsal aspect, more broadly so. Internal sac spine A absent; spine group B with one spine of medium size; spine group C with two medium-short spines.

Notes about habitat.-- All specimens were taken from foliage in a fallen tree and on vegetation.

Geographical distribution (Map 12).-- This species is known only from the Gulf Versant of México, between the Tropic of Cancer and the Isthmus of Tehuantepec.

Chorological affinities.-- *C. foveolata* and its adelphotaxon, *C. nigroviridis* - *C. teutonica*, are allopatric, but the ranges of this species and *C. nigroviridis* may overlap.

Phylogenetic relationships (Fig. 36).-- This species is the postulated adelphotaxon of the *C. nigroviridis* - *C. teutonica* lineage.

Material examined.-- Type material only; see above for details.

Coptodera nigroviridis, new species
Figs. 23H, 24K & 24L; Map 12

Type material.-- HOLOTYPE male, labelled: MEXICO, Chiapas, Pq. Montebello, Laguna Pojoj, 12.VI.1989.H.Howden [USNM]. ALLOTYPE female, labelled: MEX. Hidalgo Rte.105, 3.2km.n. Tlanchinol 1540m. in vegetation June 23. 1975; MEX. EXP. 1975 G.E. Ball & H.E. Frania collectors [USNM].

Type locality.-- Parque Montebello, state of Chiapas, México.

Derivation of specific epithet.-- From Latin *niger* and *viridis*, in allusion to the dark, black-green color of this species.

Description.-- Character states of the *C. festiva* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head brunneous to rufo-piceous; pronotum brunneous to rufo-piceous with broad testaceous lateral margins; elytra brunneous to rufo-piceous with testaceous markings; lateral margin of elytra testaceous; antennae testaceous to rufo-brunneous; mouthparts brunneo-testaceous to rufo-piceous; appendages brunneo-testaceous to rufo-brunneous, tibiae and tarsomeres darkened, brunneous to nearly rufo-piceous. Dorsal surface with moderate green lustre. Ventral surface testaceous to brunneous with thoracic sterna brunneo-testaceous to dark brunneous (epipleuron not darkened at shoulder), sterna 4 to 6 rufo-piceous at lateral edge.

Elytra (Fig. 23H). Discal setae set in foveate punctures; interneurs finely punctate.

Male genitalia. As in Figs. 24K-24L, median lobe with membranous portion medium; apical portion medium, in lateral aspect triangular, tapered gradually, in dorsal aspect slender, parallel-

sided; apex in lateral aspect pointed, in dorsal aspect narrowly rounded. Internal sac spine A absent; spine group B with two long spines; spine group C with two long spines.

Notes about habitat.-- The allotype was collected in cloud forest on bark of a dead standing tree at 1540 m altitude.

Geographical distribution (Map 12).-- This species is known only from México: north of the Isthmus of Tehuantepec on the Gulf Versant; and south of the Isthmus on the Pacific Versant.

Chorological affinities.-- The range of this species overlaps the range of its near relative, *C. foveolata*, on the Atlantic Versant of México. However, the range of *C. nigroviridis* and its adelphotaxon, *C. rufescens* + *C. teutonica*, are separated widely.

Phylogenetic relationships (Fig. 36).-- This species is the postulated adelphotaxon of the species pair *C. rufescens* + *C. teutonica*.

Material examined.-- Type material only; see above for details.

Coptodera rufescens Buquet
Figs. 12I-12L, 23I, 24M & 24N; Map 12

Coptodera rufescens Buquet 1835: 617. Type material: not seen. Type locality: Cayenne, French Guiana.-- Chaudoir, 1869: 172.

Coptodera luteopicta Chaudoir 1850: 363. Type material: LECTOTYPE female, labelled: luteopicta type Chaud (handwritten); Ex Musaeo Chaudoir (red print); rufescens Buquet Bresil Novofrib Schaum (original box label); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Novofriburgo, Rio de Janeiro, Brazil.-- Chaudoir 1869: 172.

Note about synonymy.-- Even though we have not seen the type of *C. rufescens*, we accept Chaudoir's synonymy of *C. luteopicta*.

Description.-- Character states of the *C. festiva* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head rufo-testaceous; pronotum bicolored, testaceous with rufous marking each side of median line; elytra rufous to rufo-brunneous with testaceous markings; lateral margin of elytron testaceous to rufo-testaceous; antennae and mouthparts rufo-testaceous to rufous; femora testaceous, darkened apically; tibiae and tarsi rufous to rufo-brunneous, tibiae darkened laterally. Ventral surface testaceous to rufo-testaceous; metepisternum rufous.

Elytra (Fig. 23I). Interneurs finely punctate.

Legs. Tarsal claws long, finely denticulate in basal half.

Male genitalia. As in Figs. 24M-24N, median lobe with membranous portion medium-short; apical portion medium-long, in lateral aspect trianguloid, narrowed gradually toward apex, in dorsal aspect widened, spatulate; apex in lateral aspect narrowly rounded, in dorsal aspect broadly rounded. Internal sac spine A absent; spine group B with three thick, moderately long spines; spine group C with single thick, moderately long spine.

Ovipositor. Stylomere 2 as in Figs. 12I-12L.

Notes about habitat.-- None available.

Geographical distribution (Map 12).-- This species is known from the Southern Atlantic zone of Brazil, and from French Guiana, in South America.

Chorological affinities.-- One of the known localities for this species is close to the single locality for its adelphotaxon, *C. teutonica*. The two species may be sympatric, at least in part of their range.

Phylogenetic relationships (Fig. 36).-- This species is the postulated adelphotaxon of *C. teutonica*.

Material examined.-- We examined 3 specimens, including types, and saw non-type material from the following localities:
BRAZIL (IZWP); **Rio Grande do Sul**. Rio Grande (IZWP).

Coptodera teutonica, new species
Figs. 7D, 23J, 24O & 24P; Map 12

Type material.-- HOLOTYPE, male labelled: BRAZIL,Santa Cata- rina,Nova Teutonia I-1977 Fritz Plaumann Cal.Acad.Sci.Coll. [CAS].

Type locality.-- Nova Teutonia, state of Santa Catarina, Brazil.

Derivation of specific epithet.-- From "Teutonia" of Nova Teutonia, the type locality.

Description.-- Character states of the *C. festiva* group and the following. See Tables II, IV and VI for data about standardized body length, and ratios Hw/Pw and Pw/Pl.

Color. Head dark brunneous medially, rufo-testaceous laterally; pronotum bicolored, broad brunneous macula each side of dark testaceous marking along midline, markedly broad testaceous lateral margins, anterior and posterior margins testaceous; elytra rufo-piceous to brunneous near apex, with testaceous markings; lateral margin of elytron testaceous; antennae and mouthparts testaceous; femora and tibiae testaceous, femora darkened at apex, tibiae darkened medially; tarsi rufo-testaceous. Dark markings on dorsal surface of head and pronotum with faint green lustre; dark markings of elytra with moderate green lustre. Ventral surface testaceous, abdominal sterna 1-3 darkened laterally, thoracic sterna brunneous (elytral epipleuron brunneous).

Pronotum. As in Fig. 7D.

Elytra (Fig. 23J). Interneurs punctate.

Male genitalia. Median lobe as in Figs. 24O-24P, membranous portion medium-short; apical portion medium, in lateral aspect nearly parallel, tapered gradually toward apex, in dorsal aspect rod-like, sides parallel; apex in lateral aspect narrowly rounded, in dorsal aspect moderately broadly rounded. Internal sac spine A absent; spine groups B and C with two large spines each.

Notes about habitat.-- No information is available.

Geographical distribution (Map 12).-- This species is known only from the type locality in the Southern Atlantic zone of Brazil.

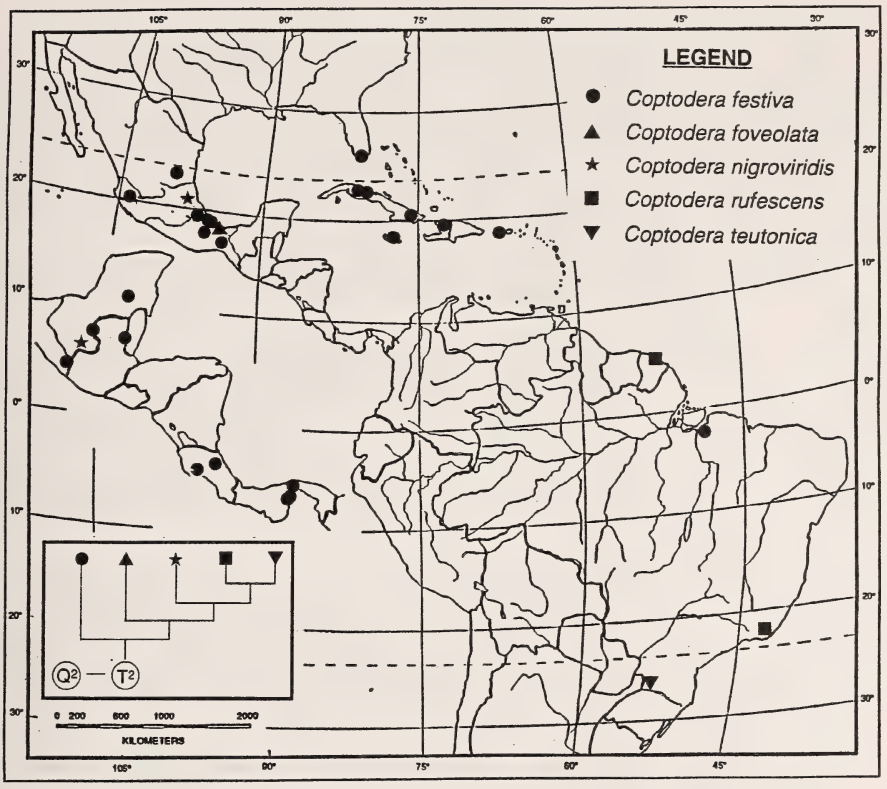
Chorological affinities.-- This species and its adelphotaxon, *C. rufescens*, may be sympatric, since both occur in the Southern Atlantic zone of Brazil.

Phylogenetic relationships (Fig. 36).-- See the topic for *C. rufescens* above, the adelphotaxon of *C. teutonica*.

Material examined.-- Type material only, see above for details.

Coptodera aeneorufa Group

This group has a single species with the character states of the *C. festiva* group, except the labrum is slightly wider than long and the elytra are unicolorous. See Table I for features of mandibles. Male genitalia with median lobe pleuropic-left; membranous portion medium-long; internal sac with macrospines (Figs. 25A-25B). Ovipositor with ensiform setae of stylomere 2 on



MAP 12. Geographical distribution of *Coptodera festiva* Dejean, *C. foveolata*, new species, *C. nigroviridis*, new species, *C. rufescens* Buquet and *C. teutonica*, new species. Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

dorsal margin (cf. Fig. 12I); nematiform setae present. The geographical range of this group includes the Amazon Basin and Surinam in South America.

Chorological affinities.-- The geographical range of the *C. aeneorufa* group is broadly overlapped by the combined ranges of its adelphotaxa, the *C. bifasciata*, *C. emarginata*, *C. picea* and *C. aerata* groups (Maps 13-20).

Phylogenetic relationships (Fig. 35).-- The *C. aeneorufa* group is the adelphotaxon of the *C. bifasciata* - *C. aerata* group lineage.

Coptodera aeneorufa Bates
Figs. 25A & 25B; Map 13

Coptodera aeneorufa Bates 1869: 76. Type material: LECTOTYPE (here selected) male, labelled: Ega (handwritten); TYPE (red paper); aeneorufa Bates (handwritten); chalcoptera Chaud

(handwritten); Ex Musaeo H.W. Bates 1892; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega (=Tefé), Amazonas, Brazil.-- 1870: XVI.

Coptodera chalcoptera Chaudoir 1869: 184. Type material: LECTOTYPE (here selected) male, labelled: LECTO (red paper); TYPE (red paper); ♂; Ex Musaeo Chaudoir; chalcoptera Chaud; Coptodera chalcoptera Chaud det. G.E. Ball '87; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega (Tefé), Amazonas, Brazil.-- Bates 1870: XVI.

Note about synonymy.-- Based on study of type material, we confirm the synonymy proposed by Bates, of the names *C. aeneorufa* and *C. chalcoptera*.

Description.-- Character states of the *C. aeneorufa* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head brunneo-testaceous to rufo-brunneous; pronotum brunneo-testaceous to rufo-brunneous, with a rufo-brunneous to brunneous spot each side of mid-line; elytra dark brunneo-testaceous to brunneous, with faint greenish to aeneous lustre; lateral margins of elytra testaceous to rufo-testaceous; appendages, antennae, and mouthparts testaceous to brunneo-testaceous, tibiae darkened. Ventral surface testaceous to brunneo-testaceous except proepisternum (medially), mesepisternum, mesepimeron, metasternum (laterally), metepisternum, and epipleuron at shoulder brunneo-testaceous to rufo-brunneous.

Elytra. Interneurs impunctate.

Male genitalia. As in Figs. 25A-25B, median lobe with apical portion medium, in lateral aspect trianguloid, tapered gradually toward apex, in dorsal aspect, trianguloid; apex in lateral aspect narrowly rounded, in dorsal aspect, pointed, apex bent to right. Internal sac spine A elongate; spine group B with three large spines; spine group C with single large spine.

Notes about habitat.-- Specimens were taken in primary (lowland tropical evergreen) forest in Brazil and in cis-Andean Peru on tree trunks, along a trail.

Geographical distribution (Map 13).-- The range of this species includes the Amazon Basin and Surinam in South America.

Chorological affinities and phylogenetic relationships.-- See these topics for the *C. aeneorufa* group, above.

Material examined.-- We examined 34 specimens, including types, and saw non-type material from the following localities:

BOLIVIA La Paz. Coroico (IZWP); Tumupasa (USNM). Collection was made in December.

BRAZIL Amazon (BMNH); Amazons (BMNH); **Amazonas**. 5 km w Alvaraes (CMNH); Ega (BMNH)(MNHP); **Para**. (CMNH)(MNHP); Belem (ZSMM); Bragance (MNHP); Santarem (MNHP). Collections were made in June, October, and February.

ECUADOR Napo Pastaza. 30 km e Lago Agrio, Via a Tarapoa (USNM). Collection was made in October.

PERU Huánuco. Monzon Valley, Tingo Maria (CAS); **Madre de Dios**. Pakitza, 12°07'S 70°58'W (USNM). Collections were made in October and November.

SURINAM Inini. Saül (ZSMM). Collection was made in March.

Coptodera bifasciata Group

This group has four species with character states of the *C. festiva* group, except the labrum is as wide as long to slightly wider than long. See Table I for features of mandibles. Male genitalia with median lobe pleuropic-right; membranous portion various degrees of "medium";

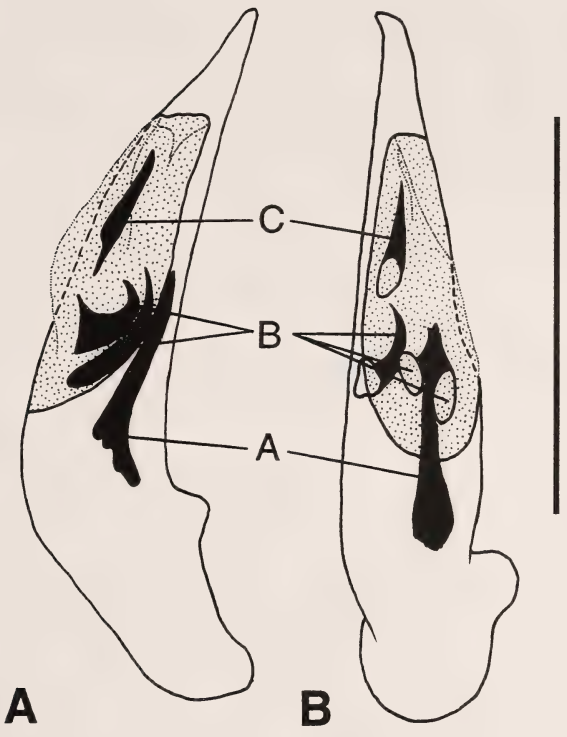


FIGURE 25. Line drawings of male genitalia of *C. aeneorufa* Bates. Fig. A left lateral aspect. Fig. B dorsal aspect. Scale bars = 1 mm. Legend: A, spine A; B, spine B; C, spine C.

internal sac with macrospines (Figs. 27A-27H). The geographical range of this group extends from the Southern Atlantic zone of South America, north through the Amazon Basin, and Lower and Nuclear Central America to the Gulf Versant of México north of the Isthmus of Tehuantepec (Map 14).

Chorological affinities.-- The geographical range of the *C. bifasciata* group is broadly overlapped by the combined ranges of its relatives, the *C. emarginata* + *C. picea* + *C. aerata* groups (Maps 14-20).

Phylogenetic relationships (Fig. 35).-- The *C. bifasciata* group is the postulated adelphotaxon of the *C. emarginata* group.

MAP 13. Geographical distribution of *Coptodera aeneorufa* Bates. Inset indicates phylogenetic relationship of species as illustrated in Fig. 36.

Coptodera bifasciata Putzeys
Figs. 26A, 27A & 27B; Map 14

Coptodera bifasciata Putzeys 1845: 394. Type Material: HOLOTYPE female, labelled: type (hand written); Ex Musaeo Chaudoir (red print); TYPE (red paper); bifasciata Putzeys Brésil C.

Lacordaire Bonvouloir (box label); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: Brazil.-- Chaudoir 1869: 180.

Description.-- Character states of the *C. bifasciata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head testaceous, darkened narrowly to broadly medially; pronotum bicolored, brunneous to rufo-piceous with broad testaceous lateral margins; elytra brunneous to rufo-piceous, with testaceous markings; lateral margins of elytra testaceous; appendages, antennae, and mouthparts testaceous to brunneo-testaceous. Dorsal surface with faint greenish to aeneous lustre. Ventral surface testaceous except proepisternum (medially to totally), mesepisternum, mesepimeron, metasternum (laterally), metepisternum, and epipleuron at shoulder rufo-brunneous to brunneous.

Elytra (Fig. 26A). Interneurs impunctate.

Male genitalia. As in Figs. 27A-27B, median lobe with membranous portion medium; apical portion medium, more or less flattened, in lateral aspect trianguloid, tapered gradually toward apex, in dorsal aspect narrow, rod-like, sides more or less parallel; apex in lateral aspect pointed, in dorsal aspect narrowly rounded. Internal sac spine A long; spine group B with one long spine; spine group C with two spines of medium length.

Notes about habitat.-- No information is available.

Geographical distribution (Map 14).-- This species is recorded only from the Southern Atlantic zone of eastern Brazil.

Chorological affinities.-- The range of this species is overlapped by those of the other three species which are part of the *C. bifasciata* - *C. braziliensis* lineage.

Phylogenetic relationships (Fig. 36).-- This species is part of an unresolved trichotomy with *C. tripartita* and the *C. cupreotincta* + *C. braziliensis* lineage.

Material examined.-- We examined 9 specimens, including types, and saw non-type material from the following localities:

BRAZIL (BMNH); **Minas Gerais**. Caraça (MNHP); Rio Piracicaba (MNHP); **Santa Catarina**. (BMNH); **São Paulo**. Peruhybe (IZWP). Collection in February.

Coptodera tripartita Chaudoir
Figs. 26B, 27C & 27D; Map 14

Coptodera tripartita Chaudoir 1869: 180. Type material: LECTOTYPE (here selected) male, labelled: (blue rectangle); Ex Musaeo Chaudoir (red print); TYPE (red paper); tripartita Chaud Amazone Ega Bates (original box label); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega (=Tefé), Amazonas, Brazil.

Description.-- Character states of the *C. bifasciata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head testaceous, darkened narrowly to broadly medially; pronotum bicolored, brunneous to rufo-piceous with broad testaceous lateral margins, one dark spot each side of medial line; elytra brunneous to rufo-piceous, with testaceous markings; lateral margins of elytra testaceous; appendages, antennae, and mouthparts testaceous to brunneo-testaceous. Dorsal surface with faint greenish to aeneous lustre. Ventral surface testaceous except proepisternum (medially to totally), mesepisternum, mesepimeron, metasternum (laterally), metepisternum, and epipleuron at shoulder rufo-brunneous to brunneous.

Elytra (Fig. 26B). Interneurs impunctate.

Male genitalia. As in Figs. 27C-27D, median lobe with membranous portion medium-short; apical portion long, more or less flattened, in lateral aspect trianguloid, curved ventrad, in dorsal aspect slender, constricted slightly preapically; apex in lateral aspect pointed, in dorsal aspect narrowly rounded. Internal sac spine A long; spine group B two long spines; spine group C two spines, medium length.

Notes about habitat.-- Specimens were taken in a primary (lowland tropical evergreen) forest in Brazil. In Venezuela, specimens were taken by Malaise trap in a rainforest at an altitude of 140 m.

Geographical distribution (Map 14).-- This species is recorded from the Southern Atlantic zone and Amazon Basin regions of cis-Andean Bolivia, Brazil, and Venezuela.

Chorological affinities.-- The range of this species is overlapped by those of the other three species which are part of the *C. bifasciata* - *C. braziliensis* lineage.

Phylogenetic relationships (Fig. 36).-- Based on type of median lobe (anopic-pleuropic[right]), this species is part of an unresolved trichotomy, including *C. bifasciata* and *C. cupreotincta* + *C. braziliensis* lineages.

Material examined.-- We examined 32 specimens, including types, and saw non-type material from the following localities:

BOLIVIA Cochabamba. (MNHP); **La Paz**. Tumupasa (USNM). Collection was made in December.

BRAZIL (BMNH); **Amazonas**. 5 km w Alvaraes (CMNH); Ega (MNHP); Forte Boa (IZWP); 30 km w Itaquatiara, Rio Urubu (CMNH); São Paulo de Olivença (MNHP); **Mato Grosso**. Chapada (=Chapada dos Guimaraes)(CMNH); **Para**. (BMNH); Monte Alegre (AMNH); Santarem (AMNH)(BMNH)(CMNH); Tapajos (MNHP). Collections were made in September to February.

PERU Loreto. Aguaitia (MPEG). Collection in September.

VENEZUELA Amazonas. Cerro de Neblina basecamp 0°50'N66°10'W (USNM). Collection was made in February.

Coptodera cupreotincta Bates
Figs. 26C, 27E & 27F; Map 14

Coptodera cupreotincta Bates 1869: 73. Type material: LECTOTYPE (here selected) male, labelled: ♂; TYPE; amazonica Chaud; cupreotincta Bates ♂ Ega; Ex Musaeo H.W. Bates 1892; LECTOTYPE Coptodera amazonica Bts By Erwin '76; Museum Paris ex Coll R. Oberthür [MNHP]. Type locality: Ega (=Tefé), Amazonas, Brazil.-- 1883: 183.

Coptodera tesselatus Chaudoir 1869: 199. NEW SYNONYMY. Type material: LECTOTYPE (here selected) male, labelled: Mexico Klgh (handwritten); Ex Musaeo Chaudoir (red print); tesselata Chaud Mexique Dr Haag-Rntenb (original box label); LECTO- TYPE (disc with purple border); LECTOTYPE Coptodera tesselata Chaud det. George E. Ball '72; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: México.

Coptodera amazonica Chaudoir 1869: 200. Type material: LECTOTYPE (here selected) male, labelled: (green rectangle); amazonica Chaud; Ex Musaeo Chaudoir; LECTO- TYPE (disc); LECTOTYPE Coptodera amazonica Chaud det. George E. Ball '72; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega (=Tefé), Amazonas, Brazil.-- Bates 1870: XVI.

Notes about synonymy.-- Chaudoir's *C. tesselatus* was based on specimens from Mexico, which is the northern limits of *C. cupreotincta*. The two are identical, and we believe them to be

conspecific. Based on study of type material, we confirm the synonymy proposed by Bates, of the names *C. cupreotincta* and *C. amazonica*.

Comparisons.-- Males of *C. braziliensis* also have adhesive vestiture on tarsomeres 2 and 3 of the mid-leg.

Description.-- Character states of the *C. bifasciata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head testaceous, darkening medially; pronotum bicolored, brunneous with broad testaceous lateral margins; elytra dark brunneous with testaceous markings; lateral margin of elytra testaceous; appendages, antennae, and mouthparts testaceous; femora and tibiae darkened slightly medially. Dorsal surface with faint greenish to aeneous lustre. Ventral surface testaceous except mesepisternum, mesepimeron, metepimeron, and epipleuron at shoulder brunneo-testaceous to brunneous.

Elytra (Fig. 26C). Interneurs punctate.

Legs. Tarsomeres 2 and 3 of mid-leg of male with adhesive vestiture.

Male genitalia. As in Figs. 27E-27F, median lobe with membranous portion medium; apical portion medium, flattened, in lateral aspect trianguloid, tapered gradually toward apex, in dorsal aspect slender, sinuate; apex in lateral aspect pointed, in dorsal aspect narrowly rounded. Internal sac spine A long; spine group B with one long spine; spine group C with two spines of medium size.

Notes about habitat.-- In Costa Rica, specimens were taken at an altitude of 100 m; on dry wood at night. In México specimens were taken at altitudes of 121-731 m; at black light. In Panamá specimens were taken at altitudes of 243-671 m; at lights; running on underside of elevated log; on log. In Peru specimens were taken at altitudes of 290-840 m; at white and u-v light, and on trees and logs at night.

Geographical distribution (Map 14).-- This species ranges from the Amazon Basin and Southern Atlantic zone of Brazil north through Lower and Nuclear Central America to México north of the Isthmus of Tehuantepec, on the Gulf Versant.

Chorological affinities.-- The known ranges of *C. cupreotincta* and its adelphotaxon, *C. braziliensis*, do not quite meet, but these species are probably sympatric in the Southern Atlantic zone of Brazil.

Phylogenetic relationships (Fig. 36).-- Based on similarities in male genitalia and males with adhesive vestiture on mid-tarsi, this species and *C. braziliensis* are postulated to be adelphotaxa.

Material examined.-- A total of 202 specimens, including types, were examined. Non-type material was seen from the following localities:

BOLIVIA Cochabamba. MNHP.

BRAZIL (MNHP); Amazon (BMNH); Amazons (BMNH); Amazones (BMNH); **Amazonas**. (HNHM)(IZWP); Ega (BMNH)(MNHP); **Bahia**. Cachimbo (MNHP); **Para**. (CMNH); Belem (ZSMM)(USNM); **Paraiba**. (MNHP); **Rio de Janeiro**. Rio de Jan. (CMNH); **São Paulo**. Rio Pardo (MNHP). Collections in June to August, October, and December.

COSTA RICA Limón. Hamburg farm, Reventazon (BMNH)(IZWP)(USNM); Las Mercedes (USNM); Ramal Parismina (USNM). Collections in March to June and October.

MÉXICO Chiapas. 4.9 mi n Frontera Comalapa (UASM); Palenque ruins (UASM); Portugal, 7 mi se Simojovel (UCBC); **Oaxaca**. 5.6 mi s Valle Nacional, Rte. 175 (UASM); **Veracruz**. Lake Catemaco (UASM). Collections in April to August.

NICARAGUA Chontales. (BMNH).

PANAMA Canal Zone. Barro Colorado (MCZ)(USNM); Madden Forest (USNM); Madden Forest 9°06'N79°36'W (USNM); Madden Forest, Mi. 2.5, 9°05'N79°37'W (USNM); **Chiriqui**. Bugaba

(BMNH)(MCZ)(MNHP)(USNM); David (BMNH); Volcan de Chiriqui (BMNH); **Panamá**. Altos de Maje (HPST); Bayano Dist., 31 km e Canita (RHTC); Pozo Azul, Finca Vega, nr Las Nubes (CAS). Collections in April to August.

PERU Cuzco. Quiroz, R. Paucartambo (MCZ); **Junín**. Sani Beni, 8 km e Satipo (SEMC); **Madre de Dios**. Pakitza, 11°55'48"S 71°35'18"W (USNM); Pakitza, 12°07'S 70°58'W (USNM); Rio Tambopata Reserve, 30 km (air) sw of Puerto Maldonado (BMNH)(DHK). Collections were made in September to November.

Coptodera braziliensis, new species
Figs. 26D, 27G & 27H; Map 14

Type material.-- HOLOTYPE male, labelled: Hansa Humboldt S. Cat. Braz. A. Maller (hand printed) [MCZ]. ALLOTYPE female, labelled: Nova Teutonia, Sta. Cat., Brazil 30 May 41 F. Plaumann [MCZ]. 7 PARATYPES, sex and label data as follows: 1 male: Cauna S.Cath.,Brazil Dec. 1948; A. Maller, Coll. Frank Johnson Donor [AMNH]. 1 male: Nova Teutonia Santa Catarina BRAZIL IX.21.52 Fritz Plaumann [MCZ]. 1 male: BRASILIEN Rio Grde.do Sul K.E.Hüdepohl; S.Francisco de Paula XI 1959; Coll. Hüdepohl Kat. Nr. 48/1980 [ZSMM]. 1 male: MUSEUM PARIS RIO DE CASTELNAU 1844 (green paper); green disc [MNHP]. 1 male: Brasilia; 792 27; undulata Brasil (HNHM). 1 female: MUSEUM PARIS MISIONES ENV. DE SAN-IGNACIO VILLA LUTECIA E.R. WAGNER 1910 (green paper); JUIN; SEPTEMBRE [MNHP]. 1 female: Bra. (hand printed); F.C. Bowditch Coll.; Coptodera, bifasciata, Ptz (hand written) [MCZ].

Type locality.-- Hansa Humboldt (=Corupá), state of Santa Catarina, Brazil.

Derivation of specific epithet.-- Latinized name of the country in which this species is found.

Description.-- Character states of the *C. bifasciata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum rufo-brunneous with faint to moderate green lustre; pronotum at times with diffusely paler lateral margins; elytra rufo-brunneous, with faint greenish to aeneous lustre, with testaceous markings; lateral margin of elytra rufo-testaceous; appendages, antennae, and mouthparts testaceous to rufo-testaceous. Ventral surface rufo-testaceous to brunneous.

Elytra (Fig. 26D). Interneurs finely punctulate.

Legs. Tarsomeres 2 and 3 of midleg of male with adhesive vestiture as in *C. cupreotincta*.

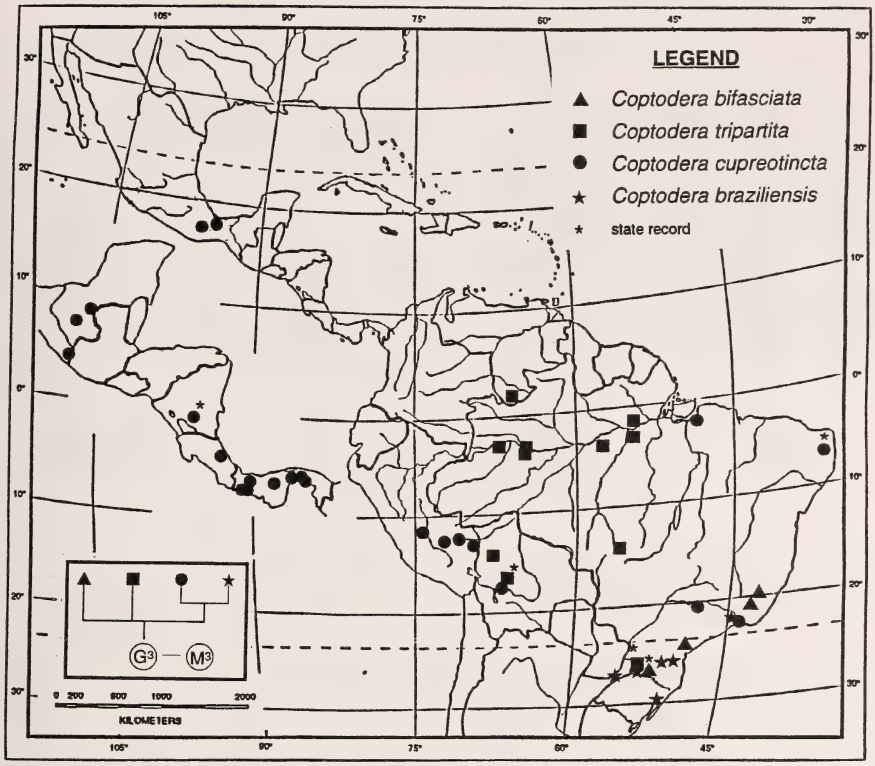
Male genitalia. As in Figs. 27G-27H, median lobe with membranous portion medium-long; apical portion medium-long, in lateral aspect trianguloid, tapered gradually toward apex, in dorsal aspect sinuate, rod-like; apex in lateral aspect pointed, in dorsal aspect narrowly rounded. Internal sac spine A long; spine group B with three long spines; spine group C with one short spine.

Notes about habitat.-- None available.

Geographical distribution (Map 14).-- This species is known only from the Southern Atlantic zone of eastern Brazil and adjacent Argentina.

Chorological affinities and phylogenetic relationships (Fig. 36).-- See these topics for *C. cupreotincta* above, the adelphotaxon of *C. braziliensis*.

Material examined.-- Type material only; see above for details.



MAP 14. Geographical distribution of *Coptodera bifasciata* Putzeys, *C. tripartita* Chaudoir, *C. cupreotincta* Bates and *C. braziliensis* new species. Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

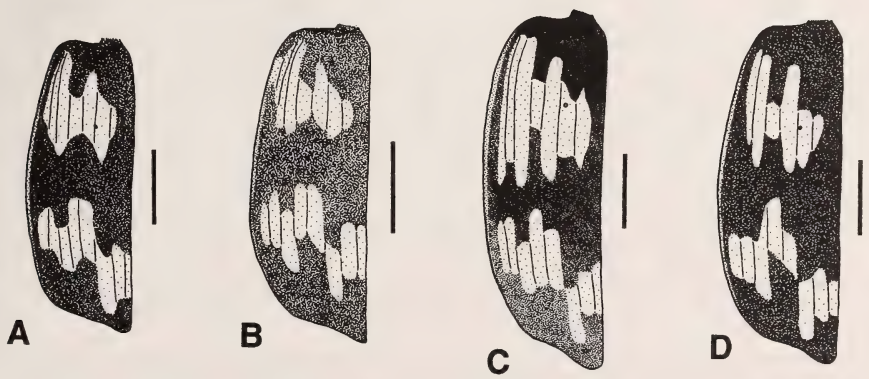


FIGURE 26. Line drawings of left elytron of *Coptodera bifasciata* group, dorsal aspect. Fig. A: *C. bifasciata* Putzeys. Fig. B. *C. tripartita* Chaudoir. Fig. C: *C. cupreotincta* Bates. Fig. D: *C. braziliensis* new species. Scale bars = 1 mm. Legend: A, spine A; B, spine B; C, spine C.

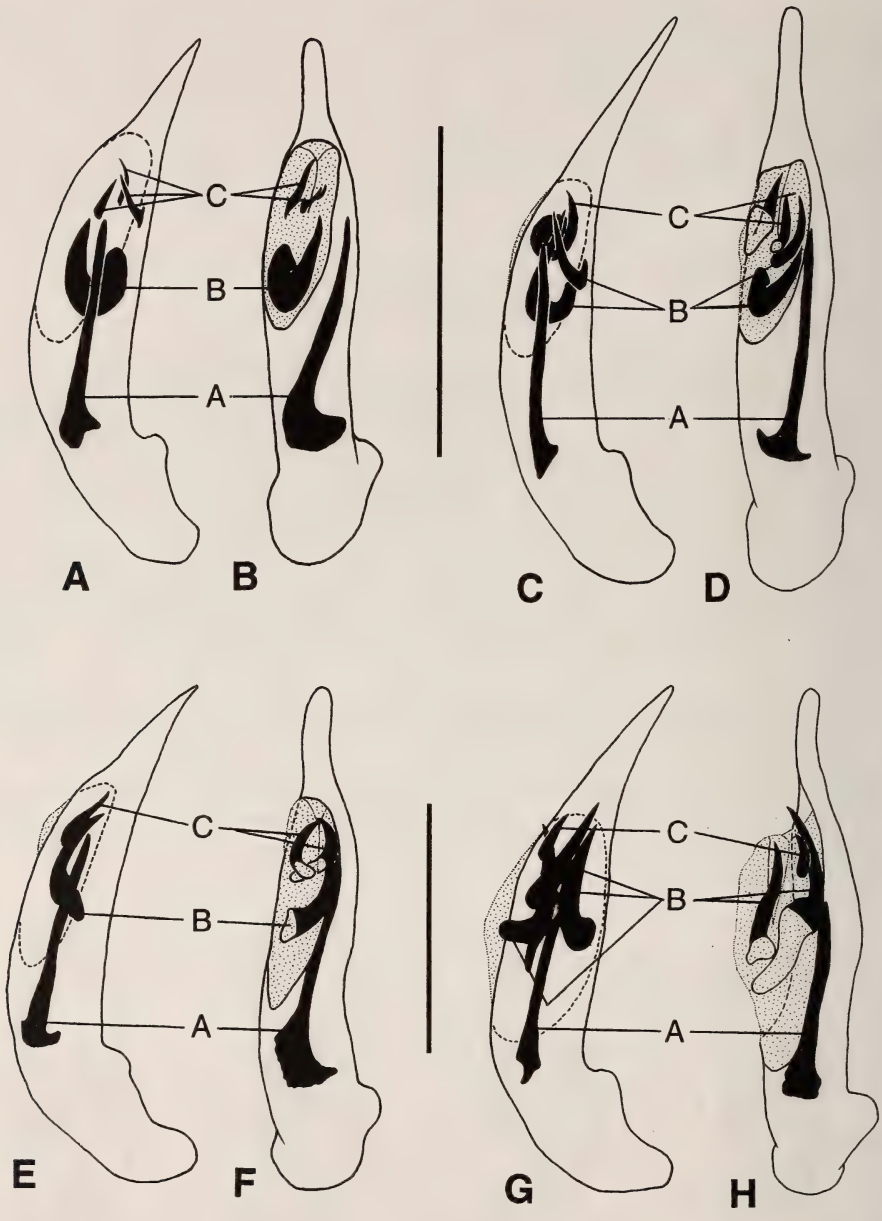


FIGURE 27. Line drawings of male genitalia of *Coptodera bifasciata* group. Figs. A, C, E & G left lateral aspect. Figs. B, D, F & H dorsal aspect. Figs. A-B: *C. bifasciata* Putzeys. Figs. C-D: *C. tripartita* Chaudoir. Figs. E-F: *C. cupreotincta* Bates. Figs. G-H: *C. braziliensis*, new species. Scale bars = 1 mm.

Coptodera emarginata Group

This group has three species with character states of the *C. festiva* group, except the anterior margin of the labrum (slightly wider than long) is more emarginate in some species (indicated in the species description), and the elytra are metallic and unicolorous rather than variegated. See Table I for features of mandibles. Male genitalia with median lobe anopic to pleuropic-right; membranous portion medium-long to long. The geographical range of this group extends from South America north through Central America into México.

Chorological affinities.-- The geographical range of the *C. emarginata* group is broadly overlapped by the combined ranges of its adelphotaxon, the *C. bifasciata* group (Map 14 and 15).

Phylogenetic relationships (Fig. 35).-- This group is the postulated adelphotaxon of the *C. bifasciata* group.

Coptodera chalcites Bates
Figs. 28A, 28C & 28D; Map 15

Coptodera chalcites Bates 1869: 75. Type material: LECTOTYPE (here selected) male, labelled: Ega (handwritten); TYPE (red paper); chalcites Bates ♂; Ex Musaeo H.W. Bates 1892; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega (=Tefé), state of Amazonas, Brazil.-- 1870: XVI.

Coptodera aeneocuprea Chaudoir 1869: 177. Type material: LECTOTYPE (here selected) male, labelled: LECTO (red paper); TYPE (red paper); (green rectangle); aeneocuprea Chaud (handwritten); Ex Musaeo Chaudoir (red print); Coptodera aeneocuprea Chaud det. George E. Ball '87; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega (=Tefé), state of Amazonas, Brazil.-- Bates 1870: XVI.

Note about synonymy.-- Based on study of type material, we confirm the synonymy proposed by Bates, of the names *C. chalcites* and *C. aeneocuprea*.

Description.-- Character states of the *C. emarginata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head, pronotum and elytra rufo-brunneous to dark brunneous; antennae and mouthparts rufous; appendages rufo-brunneous. Dorsal surface of elytra with faint to moderate green, aeneous or violaceous lustre, faint on the pronotum. Ventral surface rufo-brunneous.

Mouthparts. Anterior margin of labrum moderately emarginate medially.

Elytra. Interneurs punctate; apex with sutural angle broadly rounded (Fig. 28A).

Male genitalia. As in Figs. 28C-28D, median lobe with membranous portion medium, dorsal, anopic; membranous area partially sclerotized near apex. Apical portion medium-short, in lateral aspect trianguloid, slender, tapered gradually toward apex, in dorsal aspect broadly trianguloid, tapered gradually; apex in lateral aspect pointed, in dorsal aspect moderately rounded. Internal sac spine A absent; spine group B two medium size spines; spine group C two medium-small sized spines.

Notes about habitat.-- Specimens were taken in Ecuador at an altitude of 100 m; under bark of fresh cut tree and from the canopy of a fallen tree. In Peru, specimens were taken at altitudes of 200 and 290 m; at light, at white light, on logs and running on bark of a fallen dead tree.

Geographical distribution (Map 15).-- This species is recorded from cis-Andean South America in the western and central parts of the Amazon Basin.

Chorological affinities.-- The range of *C. chalcites* is overlapped by that of one of its relative, *C. acutipennis*.

Phylogenetic relationships (Fig. 36).-- This species is postulated to be the adelphotaxon of *C. emarginata* + *C. acutipennis*, based on form of the median lobe.

Material examined.-- We examined 42 specimens, including types, and saw non-type material from the following localities:

BRAZIL Amazons (BMNH); **Amazonas**. Ega (BMNH)(MNHP); Fonte Boa (BMNH); Tonantins (MNHP); **Para**. Santarem (CMNH)(IZWP).

COLOMBIA Amazonas. Leticia (CNC). Collection in July.

ECUADOR Napo Pastaza. Ashuara, on Rio Macuma, 10 km from Rio Morona (UASM); Limoncocha (HHES)(UASM). Collections were made in January, April, and July.

PERU Cuzco. Quiroz, R. Paucartambo (MCZ); **Junín**. Chanchamayo (MNHP); **Loreto**. Pebas (MNHP); **Madre de Dios**. Pakitza, 11°55'48"S 71°35'18"W (USNM); Pakitza, 12°07'S 70°58'W (USNM); 15 km ne Puerto Maldonado (SEMC); Rio Tambopata Reserve, 30 km (air) sw Puerto Maldonado, 12°50'S 69°20'W (DHK). Collections were made in June, July and September to November.

Coptodera emarginata Dejean
Figs. 28B, 28E & 28F; Map 15

Coptodera emarginata Dejean 1825: 276. Type material: HOLOTYPE male, labelled: emarginata m in Brazilia (Dejean's handwriting on green paper); Ex Musaeo Chaudoir (red print); TYPE (red paper); emarginata Dejean Bresil Coll Dejean (original box label); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: Brazil.-- Chaudoir 1869: 175.

Lebia aenea Buquet 1834: 673. Type material: not seen. Type area: French Guiana.

Coptodera aenea: Chaudoir 1869: 175.

Note about synonymy.-- We accept Chaudoir's synonymy of *C. aenea*.

Description.-- Character states of the *C. emarginata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head, pronotum and elytra rufo-brunneous to dark brunneous; antennae and mouthparts brunneous; femora dark testaceous to rufo-brunneous, darkened apically; tibiae and tarsi brunneous. Dorsal surface of head and pronotum with moderate green lustre; elytra with moderate green lustre basally gradually fainter towards apex. Ventral surface brunneous; epipleuron dark testaceous.

Mouthparts. Anterior margin of labrum shallowly emarginate medially.

Elytra. Interneurs finely punctulate; apex with lateral and sutural angles spinose; apical margin sinuate before sutural angle (Fig. 28B).

Male genitalia. As in Figs. 28E-28F, median lobe with membranous portion long, lateral-right, pleuropic. Apical portion medium-long, more or less flattened, in lateral aspect broadest at base, abruptly narrowed, then sides parallel, in dorsal aspect rod-like; apex in lateral aspect very narrowly rounded, in dorsal aspect moderately broadly rounded. Internal sac spine A large; spine group B two large spines; spine group C one spine of moderate size.

Notes about habitat.-- None available.

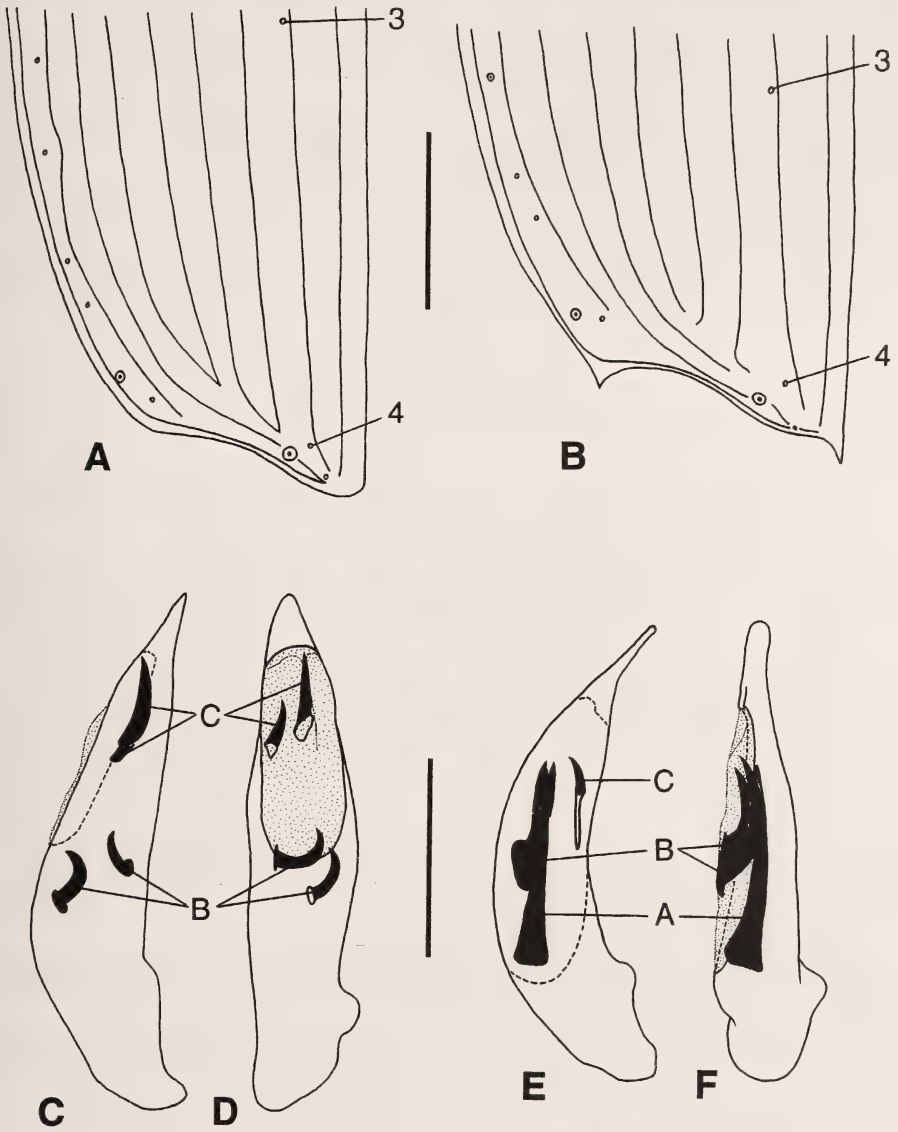


FIGURE 28. Line drawings of structures of *Coptodera emarginata* group. Figs. A-B apex of left elytron, dorsal aspect. Fig. A: *C. chalcites* Bates. Fig. B: *C. emarginata* Dejean. Figs. C & E and D & F male genitalia, left lateral and dorsal aspects respectively. Figs. C-D: *C. chalcites* Bates. Figs. E-F: *C. emarginata* Dejean. Scale bars = 1 mm. Legend: A, spine A; B, spine B; C, spine C; 3, discal setigerous puncture #3; 4, discal setigerous puncture #4.

Geographical distribution (Map 15).-- This species is known only from cis-Andean Brazil, south of the Amazon Basin, including the Southern Atlantic zone, and from Surinam in northeastern South America.

Chorological affinities.-- The geographical range of *C. emarginata* overlaps the range of its adelphotaxon, *C. acutipennis*, in Surinam.

Phylogenetic relationships (Fig. 36).-- Based on details of structure of the median lobe, *C. emarginata* is postulated to be the adelphotaxon of *C. acutipennis*.

Material examined.-- We examined 8 specimens, including types, and saw non-type material from the following localities:

BRAZIL (BMNH)(MNHP); **Goias**. Jatahy (BMNH); **Mato Grosso**. Chapada (=Chapada dos Guimaraes)(CMNH); **Minas Gerais**. Lambary (USNM); **São Paulo**. Riberão Prêto (MZSP). Collections were made in September and April.

Coptodera acutipennis (Buquet)

Figs. 1F, 6B, 6F, 11A-11D, 13B, 29A-29P, 30A-30L, 31A & 31B; Map 15

Lebia acutipennis Buquet 1834: 674. Type material: not seen. Type area: headwaters of the Oyapock River, French Guiana.-- Chaudoir, 1869: 176.-- Bates 1870: XVI; 1883: 181.

Coptodera acutipennis: Chaudoir 1869: 176.

Coptodera spinipennis Bates 1869: 75. Type material: LECTOTYPE (here selected) male, labelled: acutipennis Buq. sec. Chd.; spinipennis Bates Ega ♂; Ex Musaeo H.W. Bates 1892; Museum Paris ex Coll. R. Oberthür (light green paper) [MNHP]. Type locality: Ega (=Tefé), Amazonas, Brazil.-- Bates 1870: XVI.

Coptodera scintillans Bates 1878: 604. NEW SYNONYMY. Type material: HOLOTYPE female, labelled: Chontales Nicaragua (handwritten [Bates']); scintillans Bates (handwritten [Bates']); W.W. Bates Biol Cent Amer; Lectotype ♀ Coptodera scintillans Bates By Erwin '76; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: Chontales department, Nicaragua.

Note about synonymy.-- The new synonymy proposed above is based on comparison of type material of the two junior synonyms. The type material of *Lebia acutipennis* Buquet, to be expected in the Oberthür-Chaudoir collection (MNHP), is not there and evidently has been lost. We accept Bates' synonymy of *C. spinipennis*.

Description.-- Character states of the *C. emarginata* group and the following. See Tables VIII-X for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum brunneous to dark brunneous, with faint to moderate greenish to aeneous lustre; lateral margins of pronotum usually paler than pronotal disc; elytra brunneous to dark brunneous, with faint to very markedly developed greenish to aeneous lustre, lateral margins paler than elytral disc; antennae, mouthparts, and legs brunneo-testaceous to rufo-brunneous. Ventral surface brunneous to rufo-brunneous.

Mouthparts. Anterior margin of labrum shallowly emarginate to nearly straight (Fig. 1F); labium as in Figs. 6B & 6F.

Elytra. Interneurs finely punctate; apex with lateral angle sharply obtuse to spinose and sutural angles rectangular to spinose.

TABLE VIII. Variation in SBL among adults of *Coptodera acutipennis* (Buquet).

Morph	Country	N	Range	Mean
A[1]	México	1	8.83	8.83
B	México	2	8.58-9.25	8.92
C	México	2	8.33-8.42	8.38
D	Panamá	3	9.25-9.83	9.53
E	Ecuador	1	9.92	9.92
F	Peru	4	8.58-9.25	8.90
G	Peru	2	7.25-7.42	7.34
H	Bolivia	1	8.83	8.83
I	Ecuador	1	8.75	8.75
J	Bolivia	2	9.75- 9.92	9.84
J	Peru[2]	9	6.08- 7.83	6.83
J	Peru[3]	1	8.75	8.75
K	Brazil	4	9.17-10.00	9.71
K	Peru	1	8.33	8.33
L	Peru	1	7.58	7.58
M	Bolivia	1	8.25	8.25
N	Bolivia	2	8.92-9.17	9.05
-[4]	Panamá	2	6.67-7.00	6.84
-[5]	Peru	6	6.67-7.25	6.99
-	Bolivia	7	8.08-10.67	9.45
-	Panamá	8	9.50-10.08	9.78
-	México	3	8.00-10.00	8.99

[1] - alphabetical designations for males as described in text
[2] - state of Madre de Dios
[3] - state of Loreto
[4] - teneral males not dissected
[5] - sample of females from different countries (not all specimens included)

Male genitalia. As in Figs. 29A-29P, 30A-30L and 31A-31B, median lobe with membranous portion medium-long to long, dorsal, anopic to lateral-right, pleuropic. Apical portion various (for details, see below, under variation); apex in lateral aspect narrowly rounded, in dorsal aspect narrowly to moderately broadly rounded. Internal sac spine A large; spine group B absent; spine group C with one or two small to large spines (see also Figs. 11).

Female genitalia. Reproductive tract as in Fig. 13B.

Notes about variation.-- This species was very difficult to diagnose because of the variation in the male genitalia - not only the form of the median lobe, but also the number and location of spines on the internal sac. Externally, there are no visible characters to separate this complex into distinct species. Rather than name each subgroup (based on the different male genitalia) as a new species, we decided to use the designation of morphs. These designations were alphabetical, using letters A to N (Figs. 29A-29P and 30A-30L). All males were dissected except two specimens in MNHP (both from Ega, Brazil) and two extremely teneral specimens in USNM (both from Canal Zone, Panamá). Females were not grouped into these morphs, as it was not possible to associate

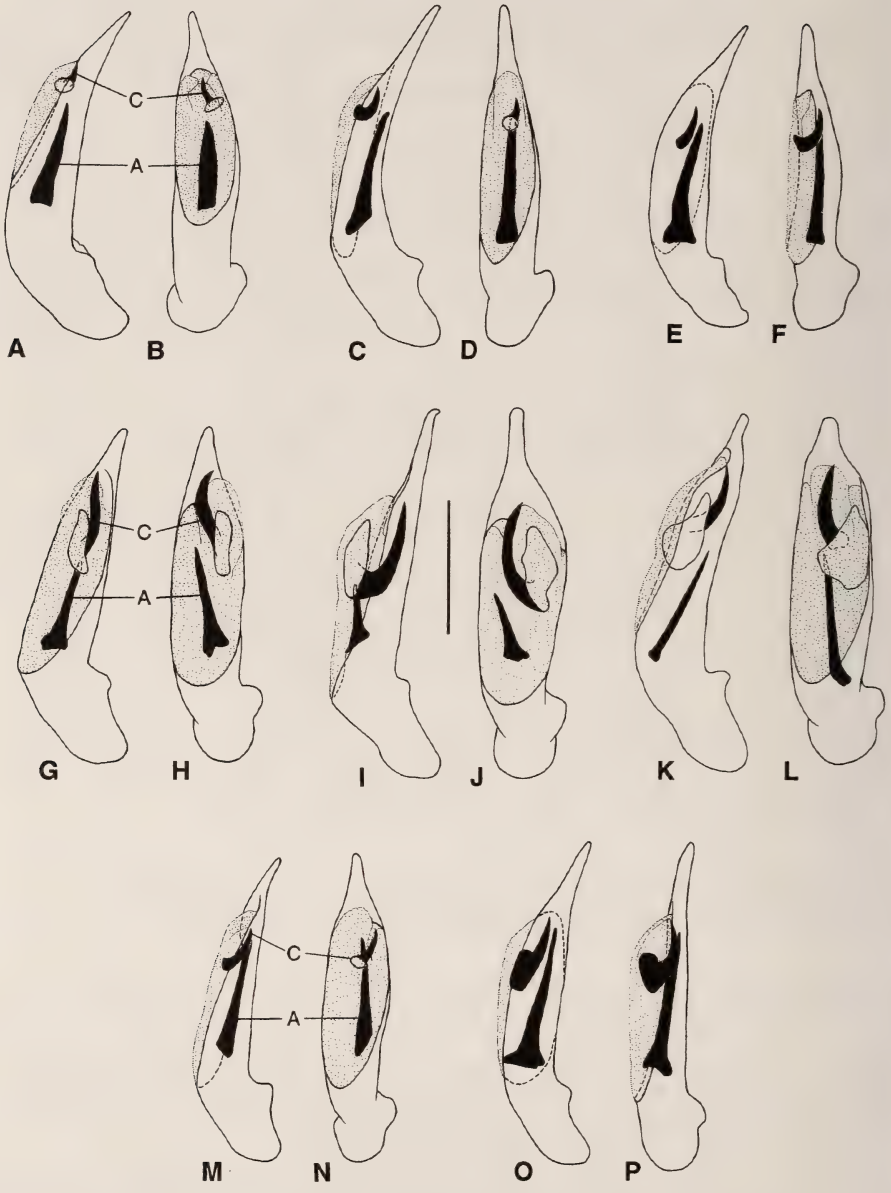


FIGURE 29. Line drawings of male genitalia of *C. acutipennis* (Buquet). Figs. A, C, E, G, I, K, M & O left lateral aspect. Figs. B, D, F, H, J, L, N & P dorsal aspect. Figs. A-B: morph A. Figs. C-D: morph B. Figs. E-F: morph C. Figs. G-H: morph D. Figs. I-J: morph E. Figs. K-L: morph F. Figs. M-N: morph G. Figs. O-P: morph H. Scale bars = 1 mm. Legend: A, spine A; C, spine C.

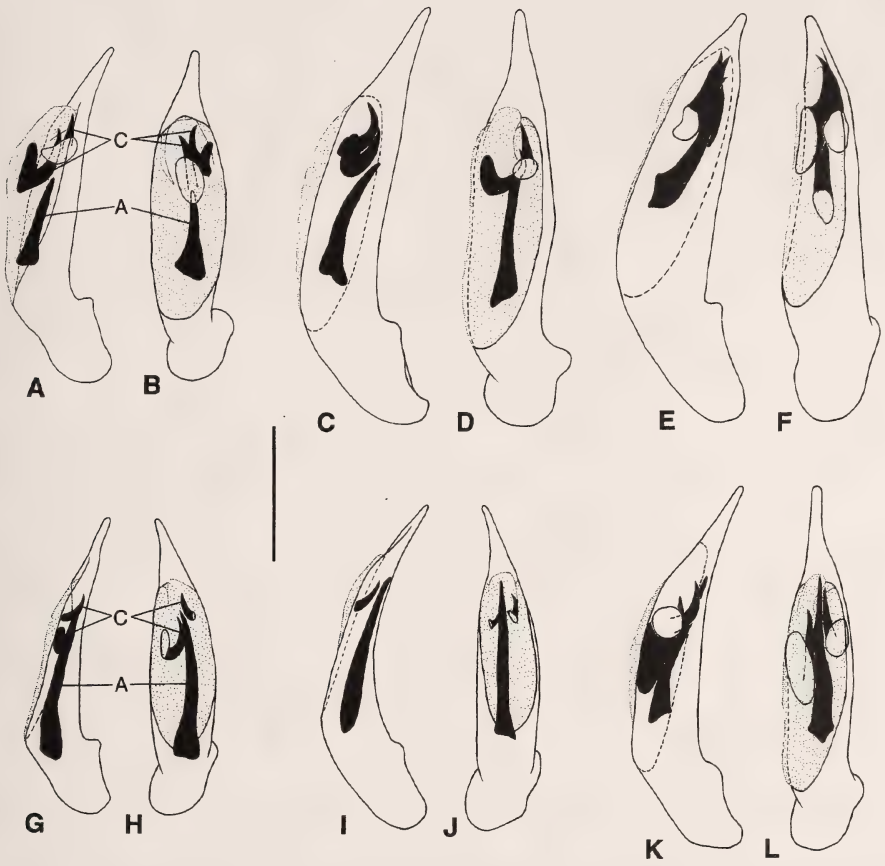


FIGURE 30. Line drawings of male genitalia of *C. acutipennis* (Buquet). Figs. A, C, E, G, I & K left lateral aspect. Figs. B, D, F, H, J & L dorsal aspect. Figs. A-B: morph I. Figs. C-D: morph J. Figs. E-F: morph K. Figs. G-H: morph L. Figs. I-J: morph M. Figs. K-L: morph N. Scale bars = 1 mm. Legend: A, spine A; C, spine C.

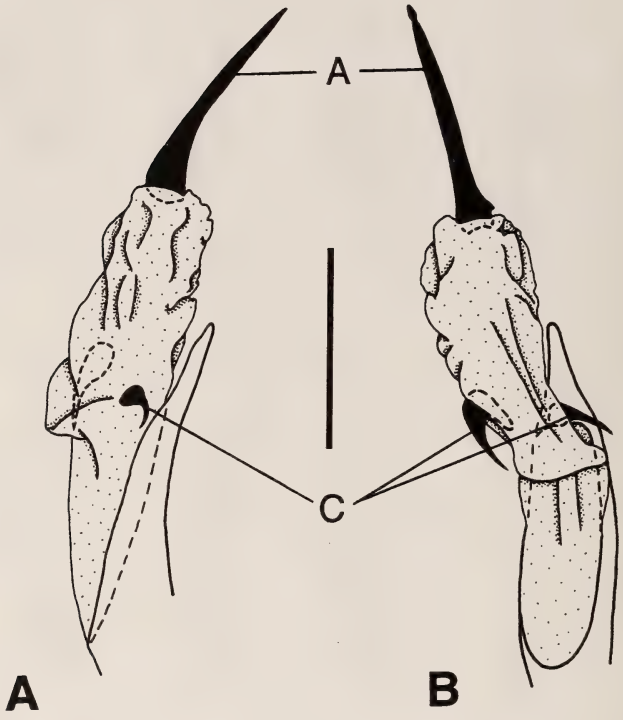
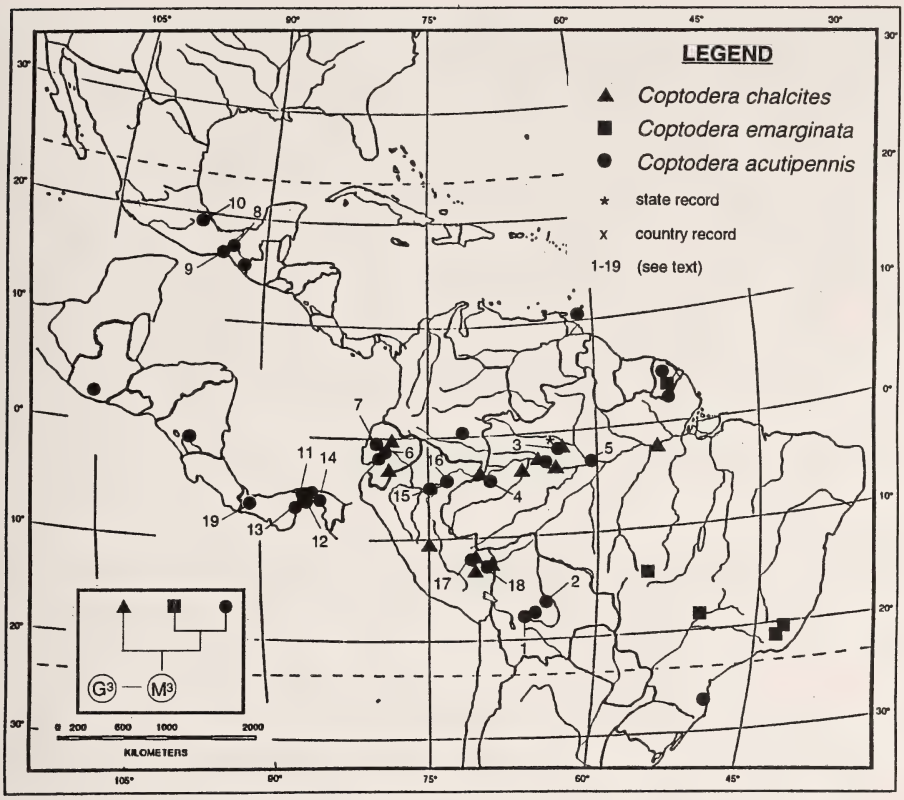


FIGURE 31. Line drawing of male genitalia of *C. acutipennis* (Buquet), morph J. Figs. A & B left lateral and dorsal aspects respectively. Scale bars = 1 mm. Legend: A, spine A; C, spine C.

them with the males when more than one type of male morph was found at a given locality. It is possible that some day molecular work will show these morphs to be distinct species.

Notes about habitat.-- Specimens were taken in Bolivia at an altitude of 430 m at fruitfalls and at rotting flood debris; in Ecuador at 100 to 280 m altitude at fruitfalls and in a Malaise-FIT trap; in México at 244 to 1010 m and at black light; in Panamá in litter along road at night, at light traps and at white and uv light; in Peru at 140 and 290 m altitude; at a figfall at night and at fermenting fruit of *Ficus* L.; and in Trinidad at 244 to 366 m altitude.

Geographical distribution (Map 15).-- The range of this species extends from the Southern Atlantic zone of southeastern South America north, from the Tropic of Capricorn, through the Amazon Basin to eastern México and the Gulf Versant, north of the Isthmus of Tehuantepec. In South America most of the range of *C. acutipennis* is cis-Andean, but one locality in Ecuador where specimens had been collected, is trans-Andean.



MAP 15. Geographical distribution of *Coptodera chalcites* Bates, *C. emarginata* Dejean and *C. acutipennis* (Buquet). Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

Chorological affinities and phylogenetic relationships (Fig. 36).-- See these topics for *C. emarginata* above, the adelphotaxon of *C. acutipennis*.

Material examined.-- We examined 93 specimens, including types, and saw non-type material from the following designated localities on Map 15 (letters and numbers following the coden indicate morph designation and number of males dissected respectively):

BOLIVIA Cochabamba. Region Chaparé (ZSMM); Villa Tunari (Loc. 1: UASM, H-1, J-1, M-1, N-2); **Sara**. (Loc. 2: MNHB, J-1). Collections in October and May.

BRAZIL Amazons (Loc. 3: BMNH, K-1), (MNHP); **Amazonas**. Benjamin Constant (Loc. 4: MZSP, K-1); Ega (MNHP); Manaus (Loc. 5: USNM, K-2); **Santa Catarina**. Hansa Humboldt (IZWP). Collection was made in September.

COLOMBIA Columb. Or. (MNHP).

COSTA RICA Puntarenas. 6 km s Sta. Elena (JEWC). Collection in June.

ECUADOR Napo Pastaza. Campana Cocha, e Puerto Misahuali (UASM); Limoncocha (Loc. 6: UASM, I-1); **Pichincha**. Rio Palenque Res. Sta., 47 km s Santo Domingo (Loc. 7: UASM, E-1)(CNC). Collections made in April to July.

FRENCH GUIANA Gourdonville (MNHP).
GUATEMALA Escuintla. Zapote (BMNH).
MÉXICO Chiapas. 1.4 km n Frontera Comalapa (UASM); 18.7 km n Ocozocuautla (Loc. 8: UASM, C-1); **Oaxaca**. 8 km e Tapanatepec, Rte. 190 (Loc. 9: UASM, B-2); **Veracruz**. Fortin de las Flores (Loc. 10: UCBC, A-1). Collections were made in June and July.
PANAMA Bocas del Toro. Almirante (USNM); Miramar 09°00'N 82°15'W (label reads Chiriqui province, which is incorrect if the latitude and longitude are correct) (Loc. 19: USNM, D-1); **Canal Zone**. Barro Colorado Is. (Loc. 11: USNM, C-1, D-2)(MCZ); Coco Solo Hosp. (Loc. 12: USNM, D-1); **Panamá**. Cerro Azul road nr Las Nubes (CAS); Cerro Campana (USNM); Cerro Campana, nr Chica (Loc. 13: UASM, C-1); dist. Chepo, Altos de Maje (Loc. 14: USNM, D-1); Ft. Gulick Rd. (USNM). Collections were made in March to May, July, September and November.
PERU Loreto. Cocha Shinguito (Loc. 15: UASM, F-4, J-1); Iquitos (Loc. 16: USNM, K-1); **Madre de Dios**. Pakitza, 12°07'S 70°58' (Loc. 17: USNM, L-1); Rio Tambopata Res. 30 km (air) sw Pto. Maldonado (Loc. 18: BMNH, G-1, J-9; CAS, G-1). Collections were made in August, November and February to April.
TRINIDAD Arima Valley (AMNH). Collection was made in November.

TABLE IX. Variation in Hw/Pw among adults of *Coptodera acutipennis* Buquet.

Morph	Country	N	Range	Mean
A[1]	México	1	0.77	0.77
B	México	2	0.76-0.77	0.77
C	México	2	0.72	0.72
D	Panamá	3	0.74-0.76	0.75
E	Ecuador	1	0.73	0.73
F	Peru	4	0.76-0.78	0.77
G	Peru	2	0.77-0.80	0.79
H	Bolivia	1	0.77	0.77
I	Ecuador	1	0.80	0.80
J	Bolivia	2	0.76-0.79	0.78
J	Peru[2]	9	0.75-0.80	0.78
J	Peru[3]	1	0.80	0.80
K	Brazil	4	0.72-0.760	0.75
K	Peru	1	0.76	0.76
L	Peru	1	0.78	0.78
M	Bolivia	1	0.82	0.82
N	Bolivia	2	0.78	0.78
-[4]	Panamá	2	0.72-0.75	0.74
-[5]	Peru	6	0.78-0.83	0.80
-	Bolivia	7	0.76-0.83	0.80
-	Panamá	8	0.73-0.79	0.75
-	México	3	0.75-0.80	0.78

[1] - alphabetical designations for males as described in text
[2] - state of Madre de Dios
[3] - state of Loreto
[4] - teneral males not dissected
[5] - sample of females from different countries (not all specimens included)

TABLE X. Variation in Pw/Pl among adults of *Coptodera acutipennis* Buquet.

Morph	Country	N	Range	Mean
A[1]	México	1	1.58	1.58
B	México	2	1.58-1.70	1.64
C	México	2	1.61	1.61
D	Panamá	3	1.62-1.71	1.65
E	Ecuador	1	1.68	1.68
F	Peru	4	1.52-1.55	1.54
G	Peru	2	1.53-1.56	1.55
H	Bolivia	1	1.48	1.48
I	Ecuador	1	1.50	1.50
J	Bolivia	2	1.55	1.55
J	Peru[2]	9	1.50-1.67	1.60
J	Peru[3]	1	1.50	1.50
K	Brazil	4	1.64-1.71	1.66
K	Peru	1	1.61	1.61
L	Peru	1	1.59	1.59
M	Bolivia	1	1.56	1.56
N	Bolivia	2	1.52-1.60	1.56
-[4]	Panamá	2	1.60-1.67	1.64
-[5]	Peru	6	1.53-1.67	1.60
-	Bolivia	7	1.52-1.62	1.57
-	Panamá	8	1.55-1.67	1.62
-	México	3	1.59-1.64	1.60

[1] - alphabetical designations for males as described in text
[2] - state of Madre de Dios
[3] - state of Loreto
[4] - teneral males not dissected
[5] - sample of females from different countries (not all specimens included)

Coptodera picea Group

This group has a single species which is characterized by finely setose labrum and clypeus, a shallowly emarginate anterior margin of labrum, which is wider than long, four discal setigerous punctures on each elytron, elytra unicolorous, reduced upper spur on inner surface of fore-tibia, and mid-tibia of male with notch on ventral surface near apex. See Table I for features of mandibles. Male genitalia with median lobe anopic; membranous portion medium-long; internal sac with macrospines (Figs. 32A-32B). Ovipositor with ensiform setae of stylomere 2 on dorsal margin (cf. Fig. 12I); nematiform setae present. The geographical range of this group is the most extensive, from cis-Andean South America, south of the Tropic of Capricorn north through Middle America to the Gulf Versant of México, south of the Tropic of Cancer, and to the tip of Florida.

Chorological affinities.-- The range of the *C. picea* group overlaps the southern part (South and Middle America) of the range of its adelphotaxon, the *C. aerata* group (Maps 16-20).

Phylogenetic relationships (Fig. 35).-- On the basis of shared apotypic features, reduced upper fore-tibial spur and anopic median lobe, this group is the adelphotaxon of the *C. aerata* group.

Coptodera picea Dejean
Figs. 4A-4F, 6C, 6G, 9C-9a, 32A & 32B; Map 16

Coptodera picea Dejean 1826: 458. Type material: LECTOTYPE (here selected) male, labelled: picea in Brazilia (Dejean's handwriting on green paper); Mannheim (Dejean's handwriting on green paper); Ex Musaeo Chaudoir (red print); TYPE (red paper); picea Dejean Brésil Coll. Dejean (Chaudoir Collection box label); LECTOTYPE ♂ Coptodera picea By Erwin '76; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: Brazil.-- Chaudoir 1869: 178.

Coptodera velox Gory1833: 195. Type material: HOLOTYPE male, labelled: velox Cayenne (Dejean's handwriting on green paper); Lacordaire (Dejean's handwriting on green paper); velox Dej. TYPE (red paper); Ex Musaeo Chaudoir (red print); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: Cayenne, French Guiana.-- Chaudoir 1869: 178.

Lebia rufula Buquet 1834: 680. Type material: HOLOTYPE male, labelled: Lebia rufula Buquet (handwritten); Ex Musaeo Chaudoir (red print); rufula Buq TYPE (red paper); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Cayenne, French Guiana.

Coptodera rufula: Chaudoir 1869: 178.

Coptodera unicolor Chevrolat 1834: No. [40]. NEW SYNONYMY. Type material: lectotype (here selected), female, labelled: Coptodera unicolor Chevr. Mexique; Chevrolat Carabidae Fr. V. d. Poll. Pres. 1909, E.B. Poulton; LECTOTYPE Coptodera unicolor Chev. By Erwin '76; TYPE Col: 126 Coptodera unicolor Chevr. HOPE DEPT. OXFORD [HECO]. Type area: México.

Coptodera obscura Laporte 1834: 51. Type material: not seen. Type locality: Orizaba, Veracruz, México.-- Chaudoir 1869: 178.

Notes about synonymy.-- The type specimen of *Coptodera unicolor* Chevrolat has the diagnostic character states of *C. picea* and we believe them to be conspecific. Based on examination of type material, we confirm the synonymy indicated by Chaudoir (1869: 178). We accept Chaudoir's synonymy of *C. obscura*.

Description.-- Character states of the *C. picea* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head, pronotum and elytra brunneous to nearly rufo-piceous; appendages, antennae, and mouthparts paler; lateral margin of elytron paler or not. Ventral surface rufo-brunneous to dark brunneous; epipleuron pale medially.

Mouthparts. Mandibles as in Figs. 4A-4F; labium as in Figs. 6C & 6G.

Elytra. Interneurs impunctate.

Legs. Fore-tibia as in Figs. 9C-9D; tarsal claws as in Fig. 9E.

Male genitalia. As in Figs. 32A-32B, median lobe with apical portion of medium length with ventral hook, hardly tapered before apex, in dorsal aspect trianguloid, slender; apex pointed in both lateral and dorsal aspects. Internal sac with spine A small; spine group B with two large spines; and spine group C absent.

Notes about variation.-- One female in a series of 15 specimens from Surinam has adhesive vestiture on tarsomeres 1 to 3 of the left front leg. The tarsomeres of the right front leg and the midtibia are unmodified.

Notes about habitat.-- Specimens were taken in the following countries at these altitudes: Bolivia, 500 m.; México, 30-880 m.; Peru, 290-840 m.; and Venezuela, 1370 m. Specimens were taken at u-v light traps in Belize and Honduras; from a Primavera log (*Cybistax* Mart. exx.

Meissn.) from Guatemala; from a light fixture in Honduras; at mercury vapor and u-v light and in bromeliads and on logs in México; by fogging the canopy with insecticide, at white light and on trails at night in Peru; by beating dead leaves in a cleared area in Trinidad; and at light in Venezuela. The Florida specimen was taken by beating dead (fire-killed) palmetto fronds in a burned pine scrub habitat.

Geographical distribution (Map 16).-- This species ranges from the Southern Atlantic zone northward through Amazonian Brazil and cis-Andean parts of South America to México north of the Isthmus of Tehuantepec, to Cuba in the West Indies, and to southern Florida.

Chorological affinities and phylogenetic relationships (Fig. 36).-- For details, see these topics for *C. picea* group above.

Material examined.-- A total of 309 specimens, including types were examined. Non-type material was seen from the following localities:

BELIZE Cayo. Augustine (CMNH); Western Hwy. Mi 66 (FSCA). Not located "M-tee dist." (MCZ). Collections in March, May, and July.

BOLIVIA (BMNH); **Beni**. 2 km n Guayaramerin (HNHM); Rurrenabaque, Rio Beni (USNM); **Sara**. Santa Cruz Dept. (MNHB). Collections in October and April.

BRAZIL (FMNH)(HNHM)(ZSMM); Amazon (MCZ); **Algoas**. São Miguel dos Campos (CMNH); **Amazonas**. Maturaca, alto Rio Cauaburi (MZSP); **Bahia**. (BMNH); **Espirito Santo**. Espirito Santo (BMNH); **Mato Grosso**. Chapada (=Chapada dos Guimaraes) (AMNH)(CMNH); **Minas Gerais**. Aguas Vermelhas (CMNH); **Para**. (BMNH); Monte Alegre (CMNH); **Rondônia**. Porto Velho, Rio Madeira (USNM); Rio Madeira, Madeira-Mamore R.R. Co. Camp 41 (USNM); **Santa Catarina**. Nova Teutonia (UASM); **São Paulo**. São Paulo (IZWP). Collections in October, December, January, and April.

BRITISH GUIANA Essequibo. Mataruki, Upper Essequibo (MCZ). Collection in December.

COLOMBIA (BMNH).

CUBA Camaguay. Camaguay (MCZ). Collection in September.

GUATEMALA Alto Verapaz. Cacao Trece Aguas (USNM); Chacoj (BMNH); Chiacaman (BMNH); Panzos (BMNH); San Cristobal Quixal (HFRE); 30 km nw San Cristobal (JEWC); **Izabal**. Cayuga (USNM); Yzabal (BMNH); **Petén**. Tikal (MZUM). One specimen ex. Guat. (USNM). Collections in April and May.

GUAYANA (MCZ).

HONDURAS (BMNH); **Atlandia**. Lancetilla, United Fruit Co. (FSCA); **Colón**. 3 mi sw Sonaguera (FSCA); **Guaimas**. Tela (MZUM). Collections in May, June, and August.

MÉXICO (BMNH)(IZWP)(MCZ); **Chiapas**. 6.3 & 7.4 km n Ocozocuautla (UASM); 16 km n Ocozocuautla (CNC); Hwy 199, 10 km s Palenque, San Manuel Rd. (LSUC); 18.3 km s Solosuchiapa, Rte. 195 (UASM); Tapachula (BMNH); 21.6 km w Tuxtla Gutierrez, Rte. 190 (UASM); **Quintana Roo**. 24 km n Carrillo Puerto (UASM); 17 km nw Felipe Carrillo Puerto (RHTC); 18-24 km n San Felipe, Carr. Pte. (JEWC); **San Luis Potosí**. Tamazunchale, Quinta Chilla (CAS); **Oaxaca**. Oaxaca (BMNH); **Tabasco**. La Chontalpa (USNM); **Veracruz**. Cerro de Plumas (="Cerro de Palmas") (AMNH)(BMNH)(MCZ); Cordova (BMNH); Cotaxtla Exp. Sta., Cotaxtla (UCBC); 15.3 km e El Tropico (UASM); Lake Catemaco (CNC); Motzorongo Sta. (MNHB); Playa Vicente (BMNH); 11.3 km n Santiago Tuxtla (UCBC); Sontecomapan (UASM); 4 km w Sontecomapan (UASM); Tuxtla (BMNH); **Yucatan**. 22 km ene Piste (RHTC). Collections in February to August and December.

NICARAGUA (BMNH); **Chontales**. (BMNH)(MCZ).

PANAMA Canal Zone. Barro Colorado Is. (USNM); Gatun (USNM); **Chiriquí**. Bugaba (AMNH)(BMNH)(MCZ)(USNM); V. de Chiriqui (BMNH)(MCZ)(USNM); Potrerillos (MCZ);

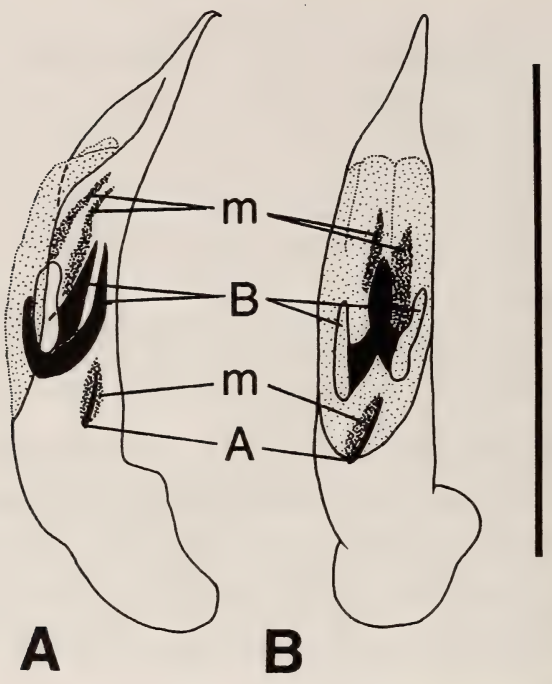
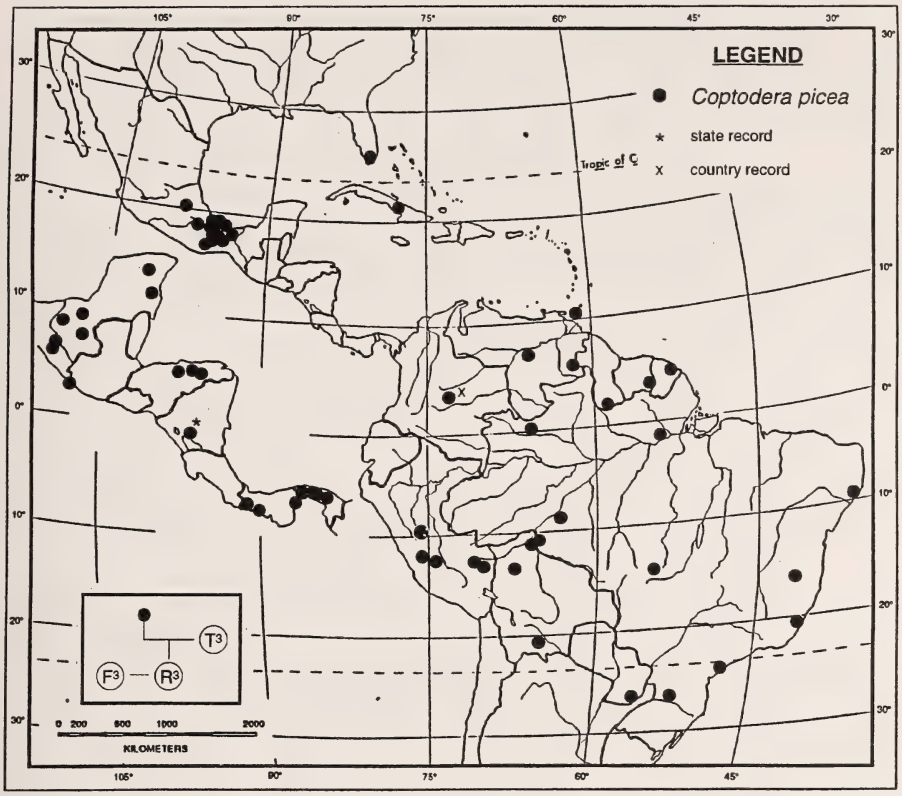


FIGURE 32. Line drawing of male genitalia of *C. picea* Dejean. Figs. A & B left lateral and dorsal aspects respectively. Scale bars = 1 mm. Legend: A, spine A; B, spine B; m, microtrichial field.

Darien. Santa Fe (OSUC); **Colon**. Sta. Rita Ridge (USNM); **Panamá**. Cabima (USNM); Cerro Campana (USNM); 11.3 mi sw Chepo (USNM); 80 km e Chepo (USNM); 11-15 km n El Llano (RHTC). Collections in April to July.
PARAGUAY Itapúa. Hohenau (IZWP); Hohenau, Alto Parana (UASM).
PERU Huanuco. Tingo Maria (AMNH); **Junín**. Chanchamayo (MNHB); Sani Beni, 8 km e Satipo (SEMC); Satipo (MCZ)(USNM); **Madre de Dios**. Pakitza, 11°55'48"S 71°35'18"W (USNM); Pakitza, 12°07'S 70°58'W (USNM); Rio Tambopata Reserve, 30 km (air) se of Puerto Maldonado 12°50'S 69°20'W (DHK)(USNM). Collections in July, and September to November.
SURINAM Marowijne. Anapaike, Rio Lawa (MZSP). Collections in November.
TRINIDAD Valencia (MCZ). Collection in May.
U.S.A. Florida. Collier Co. hwy. 41, 2.4 km. s. jct. hwy. 951 (RHTC). Collection in April.
VENEZUELA Bolivar. La Gran Sabana, Chivaton Hotel, on rd. to Kavanayen (IVIE); Suapure, Caura River (CUIC). Collections in April and June.



MAP 16. Geographical distribution of *Coptodera picea* Dejean. Inset indicates phylogenetic relationship of species as illustrated in Fig. 36.

Coptodera aerata Group

This group includes five species, characterized by a ventral sensory pit on antennomeres 5-11, finely setose labrum and clypeus, a deeply emarginate anterior margin of labrum, which is wider than long, three or four discal setigerous punctures (indicated in the species description) on each elytron, elytra unicolorous to bicolored (not a variegated color pattern), markedly reduced upper spur on the inner surface of the fore-tibia, and male mid-tibia with notch on ventral surface near apex. See Table I for features of mandibles. Male genitalia with median lobe anopic, membranous portion various in length; internal sac with macrospines (Figs. 34A-34H). Ovipositor with stylomere 2 as in Figs. 12M-12P; ensiform setae on dorsal margin; nematiform setae present. The geographical range of this group extends from north eastern United States south through México and Central America into South America, both trans- and cis-Andean, to southeastern Brazil, in the Southern Atlantic zone (Maps 17-20).

Chorological affinities and phylogenetic relationships.-- See discussion for these topics under the appropriate headings for the *C. picea* group.

Coptodera nitidula (Buquet)
Figs. 1A, 1G, 4G-4L, 9F-9H, 33A-33C, 34A & 34B; Map 17

Lebia nitidula Buquet 1834: 677. Type material: HOLOTYPE male, labelled: Ex Musaeo Chaudoir (red print); nitidula (Lebia) Buquet Brésil Sahlberg jun (original box label); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: Brazil.-- Chaudoir 1869: 185.-- Bates 1870: XVI.

Coptodera nitidula: Chaudoir, 1869: 185.

Lebia triangularis Buquet 1834: 678. NEW SYNONYMY. Type material: HOLOTYPE male, labelled: Ex Musaeo Chaudoir (red print); triangularis Buquet (Lebia) Amazone Bates (original box label); Paris Museum ex Coll R. Oberthür (light green paper) [MNHP]. Type area: Cayenne, French Guiana.

Coptodera triangularis: Chaudoir 1869: 185.

Coptodera luculenta Erichson 1847: 69. Type material: HOLOTYPE male, labelled: luculenta Erichs; Ex Musaeo Chaudoir (red print); Paris Museum ex Coll R. Oberthür (light green paper) [MNHP]. Type area: Peru.-- Chaudoir 1869: 185.

Coptodera debilis Bates 1869: 76. Type material: LECTOTYPE (here selected) female, labelled: LECTO (red paper); TYPE (red paper); S. Paulo Amaz (Bates' handwriting); debilis Bates (Bates' handwriting); nitidula Buq sec Chaud (Bates' handwriting); ex Musaeo H.W. Bates 1892; LECTOTYPE Coptodera debilis Bates det. George E. Ball '87; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: S. Paulo, Amazonas, Brazil.-- Bates 1870: XVI.

Coptodera nubiculosa Chaudoir 1869: 186. NEW SYNONYMY. Type material: LECTOTYPE male (here selected) labelled: Ex Musaeo Chaudoir (red print); TYPE (red paper); nubiculosa Chaud Paramaribo Dohrn (original box label); Paris Museum ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Paramaribo, Surinam.-- Jeannel 1949: 926.-- Reichardt 1977: 446.

Coptodera flavodisca Chaudoir 1869: 187. NEW SYNONYMY. Type material: HOLOTYPE female, labelled: (green rectangle); Ex Musaeo Chaudoir (red print); HOLO (red paper); TYPE (red paper); HOLOTYPE Coptodera flavodisca Chaud det. George E. Ball '72; flavodisca Chaud Amazons Bates (original box label); Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type locality: Ega, Amazonas, Brazil.

Coptodera flavodisca immaculipennis Bates 1883: 182. NEW SYNONYMY. Type material: LECTOTYPE (here selected), labelled: S. Geronimo Guatemala Champion; B.C.A. Col. I.1 Coptodera flavodisca, Chaud; Copt. flavodisca v. immaculipennis (Bates' handwriting); LECTOTYPE Coptodera immaculipennis Bts. By Erwin '76 [BMNH]. Type locality: San Jerónimo, Baja Verapaz, Guatemala.

Notes about type material.-- In the MNHP is a female specimen labelled as follows: Ex Musaeo Chaudoir (red print); Museum Paris ex Coll R. Oberthür (light green paper); rufodiscus Chaud Neuv. Grenada Lindig (original box label). It appears that perhaps Chaudoir intended to use "*rufodiscus*" for this species, but did not publish this name, instead publishing the name "*flavodiscus*".

Notes about synonymy.-- Adults of all of the above named forms show intermediate color patterns of the elytra, ranging from unicolorous, small pale area on darker background, darker markings on pale background (Fig. 33C), markedly pale disc (Fig. 33A) to dark diagonal markings on pale background (Fig. 33B). All of these specimens have identical male genitalia throughout the known range, and we believe them to be conspecific. The oldest available name is *C. nitidula* (Buquet), and all other names are junior synonyms.

Notes about classification.-- Jeannel (1949: 926), under the specific epithet *nubiculosa*, assigned this species to the otherwise African genus *Haplocrepis*. However, the similarities in genitalic structure among the Afrotropical and Neotropical species are considered convergent-apotypic, or symplesiotypic. As Reichardt (1977: 446) pointed out, Ball (1975) did not consider *Haplocrepis* in his ostensibly complete treatment of the New World pericaline genera.

Recognition.-- Within the *C. aerata* group, this species has the longest sensory pits on the ventral surface of antennomeres 5-11 (Fig. 1A).

Description.-- Character states of the *C. aerata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum testaceous to brunneous; elytra unicolorous, with faint greenish lustre, rufo brunneous to brunneous, or bicolored, brunneous to piceous with testaceous to brunneo-testaceous markings, lateral margin paler, testaceous to rufo-testaceous; mouthparts, antennae, and legs testaceous to rufo-testaceous. Ventral surface testaceous to dark brunneous.

Mouthparts. Labrum as in Fig. 1G; mandibles as in Figs. 4G-4L.

Elytra (Figs. 33A-33C). Interneurs impunctate to finely punctulate.

Legs. Fore-tibia as in Figs. 9F-9G; tarsal claws as in Fig. 9H.

Male genitalia. As in Figs. 34A-34B, median lobe with membranous portion medium-short to medium. Apical portion medium-short to medium, flattened, in lateral aspect trianguloid, slender, tapered to apex, in dorsal aspect trianguloid, broad; apex in lateral and dorsal aspect pointed. Internal sac spine A large; spine group B two medium to large spines; spine group C one spine of medium size.

Notes about variation.-- This species has several elytral color patterns, three of them are shown in Figs. 33A-33C.

Notes about habitat.-- Specimens were taken in the following countries at these altitudes: Bolivia, 400 m.; Brazil, 100 m.; Costa Rica, 600-1100 m.; Ecuador, 250-305 m.; Guatemala, 914-1706 m.; México, 975-1548 m.; Panamá, 243-1524 m.; Peru, 200-2300 m.; United States, 1158-1737 m. Specimens were taken in an inundation forest in Bolivia; under bark and in fibres of cut wood in Brazil; under bark in Costa Rica (and on dry bark), México and Panamá; at uv light in Costa Rica and México; in bromeliads in México; at lights in Panamá and United States; in Peru, at molasses traps, under bark and under rotting log in sandy soil; in Surinam, on a fresh cut stump of *Simarouba* Aubl.; and in United States, at mercury vapor lights and on a dead oak at night.

Geographical distribution (Map 17).-- This species ranges from Arizona in southwestern United States south through México on Pacific and Gulf Versants, through Middle America to the Chacó area of trans-Andean Ecuador, and to the Southern Atlantic zone of eastern Brazil.

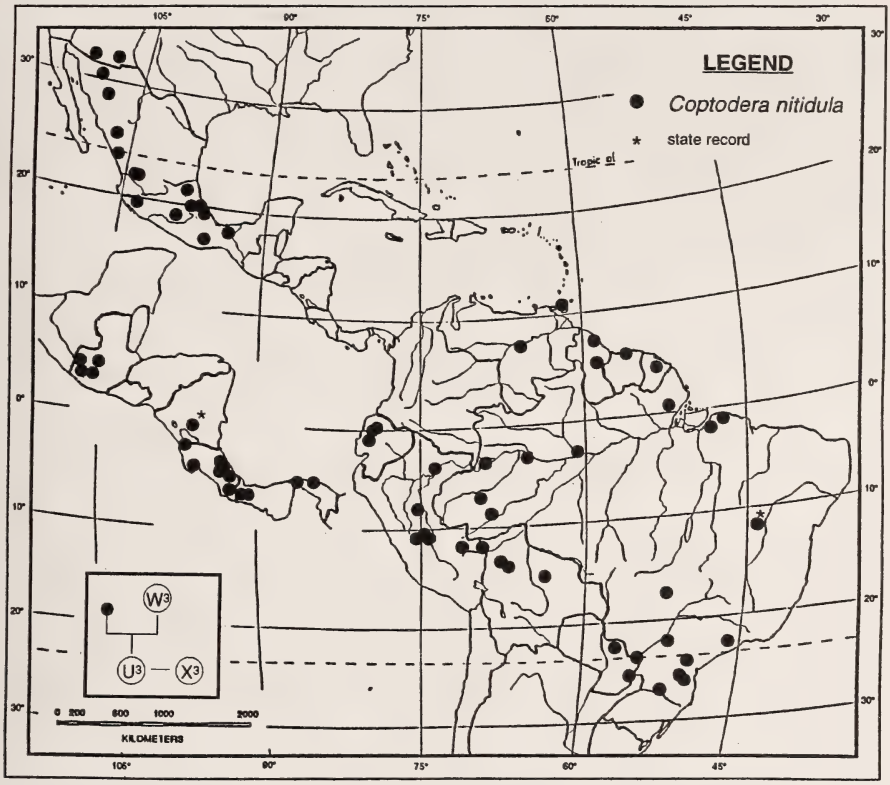
Chorological affinities.-- The geographical range of this species overlaps broadly the ranges of its adelphotaxon *C. brunnea* + *C. waytkowskii*.

Phylogenetic relationships (Fig. 36).-- *Coptodera nitidula* is postulated to be the adelphotaxon of *C. brunnea*.

Material examined.-- A total of 264 specimens, including types, were examined. Non-type material was seen from the following localities:

ARGENTINA Misiones. Gob. Misiones (MNHB).

BOLIVIA Beni. Rurrenebaque (CAS); 40 km e San Borja, Estacion Biologica Beni, Palm Camp at Rio Curiraba (USNM); **Cochabamba**. (MNHP); Region Chaparé (ZSMM); **La Paz**. Tumupasa (USNM); **Santa Cruz**. Buena Vista (FSCA). Not located: R. Japacani (CMNH). Collections were made in September, December and January.
BRAZIL Amazon (BMNH); Amazons (BMNH); S. Brazil (MCZ); **Amapa**. Pôrto Santana (USNM); **Amazonas**. Ega (MNHP); Manaus, 1 km w Taruma Falls (CMNH); AM 010, km. 26, Reserva Ducke (USNM); São Paulo de Olivença (MNHP); **Bahia**. (MNHP); **Goiás**. Jatahy (MNHP); **Mato Grosso**. Xingu (MZSP); **Para**. (BMNH)(MNHP); Belem (ZSMM); Bragance (MNHP); **Parana**. Londrina (MCZ); Rondon (MCZ); **Rondônia**. Rio Madeira (USNM); Rio Madeira, Madeira-Mamore R.R. Camp 41 (USNM). **Santa Catarina**. (MNHP); Cauna (AMNH); Corupa (AMNH); Hansa Humboldt (BMNH)(MCZ); Nova Teutonia (BMNH)(MCZ); **São Paulo**. (MNHP); Barueri (MZSP). Collections in September to January, March to May, and July.
COLOMBIA (MNHP).
COSTA RICA Alajuela. Peñas Blancas (UASM); Rio Sarapiqui, 6 air km s San Miguel (UCBC); **Cartago**. 3 km se Turrialba (UCBC); Turrialba (UASM); **Guanacaste**. Carillo (USNM); **Limón**. Hamburg farm (USNM); Hamburg farm, Reventazon (IZWP); Valle de la Estrella Pandora (UASM); **Puntarenas**. 14 km s San Vito de Java (USNM); **San José**. San Carlos (USNM). Collections in January to July, September, and October.
ECUADOR Bolívar. Chimbo (BMNH); **Pichincha**. Rio Palenque (UASM); Rio Palenque, 47 km s St. Domingo (CNC)(UASM); Rio Palenque Station, 47 km s Sto. Domingo (CNC)(UASM); Tinlandia, 17 km e Santo Domingo de los Colorados (UASM). Collections in February, May and July.
GUATEMALA Alta Verapaz. Balheu (BMNH)(MNHP)(USNM); S. Geronimo (BMNH)(MNH) (USNM); Tamahú (BMNH)(MNH); **Chimaltenango**. Mun. Yepocapa (FMNH); **Escuintla**. Zapote (BMNH); **Sacatepéquez**. Capetillo (BMNH); **San Marcos**. El Tumbador (BMNH); El Zumbador (MNHP). Collections in May.
GUYANA Essequibo. Essequibo R., Maraballi Creek (IZWP). Collections in August.
MÉXICO (BMNH)(IZWP); **Chiapas**. 18.7 km n Ocozocuautla (UASM); **Colima** se slope of Mt. Colima (CAS); **Morelos**. 8.7 km e Cuernavaca (UASM); 14.6 km e Cuernavaca, Canyon de Lobos (UASM); **Nayarit**. Arroyo Santiago, nr Jesus Maria (UCBC); La Mesa de Nayar (CAS)(UCBC); **Oaxaca**. 24.8 km s Juchatengo (UASM); **Puebla**. 14.5 km se Izucar Matamoros (CNC); 24.1 km e Teziutlan (CNC); **Queretaro**. 8.3 and 26.5 km w San Luis Potosí Queretaro border, Hwy. 120 (SEMC); **Sinaloa**. 12.9 km w El Palmito (UASM); **Sonora**. 14.5 km s Cananea (FSCA); Rancho Aguajia, 16 km nw Yecora (UASM); 6.4 km ne Yecora on road to Maycoba (UASM); **Veracruz**. Cerro de Plumas (BMNH)(MNHP); Jalapa (AMNH). Collections in March, May to September, November, and December.
NICARAGUA Chontales. (BMNH)(MCZ).
PANAMA Canal Zone. Barro Colorado, Gatun Lake (USNM); Barro Colorado Is. (USNM); 5-8 mi nw Gamboa, Pipeline Road (USNM); **Chiriqui**. Bugaba (BMNH); Miramar 09°00'N 82°15'W (USNM); Ojo de Agua, 4 km n Santa Clara (UASM); V. de Chiriqui (BMNH)(MNHP); **Panamá**. Altos de Maje, dist. Chepo (HPST). Not located "Potreriles" (CAS), which may be a misspelling of Potrerillos. Collections in May to September.
PARAGUAY Alto Parana. Puerto P. Stroessner (HNHM); **Concepción**. Horqueta (MCZ); vic. Horqueta (MCZ); **Itapúa**. Hohenau (UASM). Collection in October.
PERU east Peru (MNHP); **Huánuco**. Bella Durmiente, nr Tingo Maria (UASM); Monzon Valley, Tingo Maria (CAS); Tingo Maria (AMNH)(MCZ). **Junín**. between San Ramon de Pangoa and Boca de Kiatari, 40-55 km se Satipo (AMNH); Sani Beni, 8 km e Satipo (SEMC); Satipo (IZWP)



MAP 17. Geographical distribution of *Coptodera nitidula* (Buquet). Inset indicates phylogenetic relationship of species as illustrated in Fig. 36.

(USNM); Viena (SEMC); **Loreto**. Amazon Camp, Rio Momóm, near Iquitos (CAS); **Madre de Dios**. Pakitza, 12°07'S 70°58'W (USNM); 15 km ne Puerto Maldonado (SEMC). Collections were made in April, June to August and October to December.

SURINAM Bakhuis Gebergte (UASM); Brokopondo, Baboenhol Ranch (BMNH). Collections in January, March, and August.

TRINIDAD Arima, Verdant Valle (MCZ).

U.S.A. Arizona. Santa Cruz Co. Coronado Nat. For., Walker Canyon on FSR 221, 1.4 km s Hwy 289 (UASM); Pajarito Mts., Pena Blanca (FSCA); Pajarito Mts., Peña Blanca Can. (SMC); Pajarito Mts., Walker Cn. (SMC); Peña Blanca (UASM); **New Mexico**. Hidalgo Co. Guadalupe Canyon (CAS). Collections in July to September.

VENEZUELA Bolivar. Saupure, Caura River (CUIC). Collections in March to May.

Coptodera brunnea, new species
Frontispiece; Figs. 1B, 34C & 34D; Map 18

Type material.-- HOLOTYPE male, labelled: AZ: COCHISE CO. Guadalupe Can. vii-15-78 1300M at lite McCleve [USNM]. ALLOTYPE female, labelled: same as holotype [USNM]. 149 additional PARATYPES, sex and label data as follows: 3 females: same as holotype [SMC]. 1 male and 1 female: AZ:COCH.CO. Les- lie Cn vii-11-76 ex bait trap Scott McCleve [SMC]. 1 male: AZ: COCHISE CO. Chiricahua Mts. Horseshoe Can. vi-27-78 1511M at lite McCleve. 2 females: AZ:COCHISE CO. Guadalupe Can. vi-30-77 at lite S.McCleve [SMC]. 1 female: AZ:COCHISE CO. Douglas 1241m VI-18-72 at lite S.McCleve [SMC]. 1 female: Peloncillo Mtns, 33miE Douglas, AZ 7-17-1973 at light S.McCleve [SMC]. 1 male: Chiricahua M. VII-16-59 Ar.; D.J. & J.N. Knull Collrs. [OSUC]. 1 female: Chiricahua M. VIII-7-59:Ar.; D.J. & J.N. Knull Collrs. [OSUC]. 1 female: ARIZONA Chiricahua Mts elev. 4000 ft. Aug. 3 1969 [FSCA]. 1 female: U.S.A.,Ariz. Cochise Co. Chiricahua Mt. S. Fork Cn.; Lot No 824VII-13-1964 R.H. Arnett, Jr ER. VanTassell [FSCA]. 44 males and 36 females: AZ: Cochise Co. Huachuca Mtn. Ash Canyon Rd. (1/2 m. W Hwy 92) (5100') 2-5.VIII.89 Y.Bousquet [BMNH][CNC][MCZ][MNHP]. 1 female: Miller Canyon 5000' Huachuca Mountains Cochise Co., Ariz. 1 July 1974 E.R. Hoebeke [CUIC]. 1 female: Miller Canyon 5000' Huachuca Mountains Cochise Co., Ariz. 5 July 1974 E.R. Hoebeke [CUIC]. 1 female: AZ:Pima Co' Green Valley VIII-1973 Lonczy [CAS]. 1 male: MaderaCn. Pima Co. Arizona DrLenczy VI.1976; DAVIDSON COLLECTION Donated 1989; Coptodera unicolor Chev. [CMNH]. 1 female: MaderaCn. Pima Co. Arizona DrLenczy 7.1975; DAVIDSON COLLECTION Donated 1989; Coptodera unicolor Chev. [CMNH]. 1 male: ARIZ: Pima Co. Madera Cyn. 7. 1975 Dr. R. Lenczy [CMNH]. 1 male: ARIZ: Pima Co. Madera Cyn. VI. 1976 Dr. R. Lenczy [CMNH]. 1 female: Sta. Catalina Mts. II.26.1935 Ariz. Bryant, Lot 4 [CAS]. 1 male and 1 female: AZ:STA CRUZ CO. Pajarito Mts. Pena Blanca Can vii-2-80 1191m at lite McCleve [SMC]. 1 female: AZ:STA CRUZ CO. Pajarito Mts. Pena Blanca Cn vii-30-81 1191m at lite McCleve [SMC]. 1 male: Madera Canyon Sta. Rita Mts. Santa Cruz Co. ARIZ. 4860 ft.; Collected by J.D.Marshall June 23,1963 [CUIC]. 2 males: Arizona:Santa Rita Mts. Madera Cyn. July 3 1968 [AMNH][FSCA]. 1 female: ARIZONA Sant Rita Mts. Madera Cyn. 1 Aug 1970 K.Stephen call. [AMNH]. 1 male and 1 female: U.S.A.ARIZONA Sta.Rita Mts Madera Cn.VII.1968 leg.Dr.R. Lenczy [HNHM]. 1 female: Patagonia M. VIII-3-55.Ar.; D.J. & J.N. Knull Collrs. [OSUC]. 1 female: Arizona Peña Blanca VII.16.68 [AMNH]. 1 male: Arizona; Pajarito Mts. Pena Blanca July 13 1968 [FSCA]. 1 male: ARIZONA Pajarito Mts. Pena Blanca Cyn. 13 July 1970 K.Stephen coll. [FSCA]. 1 female: ARIZONA Pajarito Mts. Pena Blanca Cyn. 11 July 1970 K.Stephen coll. [FSCA]. 1 female: Arizona:Santa Rita Mts. Madera Cyn. July 24 1968 [FSCA]. 1 male: Ariz.Santa Cruz Co. Madera Canyon,5100' Bog Spring Cp.Grd. Santa Rita Mts. D. Davis,VII-10-26-64 [USNM]. 1 female: U.S.A.,Ariz. Santa CruzCo Pajarito Mts Pena Blanca Black light; Lot No.176 VII-26-1964 Evening J.Stibick [USNM]. 1 male: ARIZONA:St. Cruz Co. 3.2 Km S.Pena Blanca Lake.1250 m., VII-28-1989: R.S. Anderson & S.McCleve: UV light [TAMU]. 1 male: Santa Rita Mts. Ariz. 5 to 8000ft. July. F.H. Snow.; 10; H. C. FALL COLLECTION [MCZ]. 2 males: 6000ft Mt. Washington NogalesAriz. VII-20-1919; Van Dyke Collection [CAS]. 1 male: 6000ft Mt. Washington NogalesAriz. VII-19-1919; Van Dyke Collection [CAS]. 1 male and 2 females: USA AZ,SantaCruz Co. Coronado N.Forest Walker Cyn. on FSR 221.1.4km S. Hwy 289 11.VIII.89 Pollock; at black & Hg-vapor lights [UASM]. 3 females: Ariz. Santa Cruz Co. .5 mi. W Upper White Rock Cmgd., 27 July 1989 R. Turnbow [RHTC]. 1 female: NM: Chaves Co. Bottomless Lakes S.P., 7.VIII.89 Y.Bousquet [gypsum flats] [CNC]. 1 female: MEXICO. Chiapas 5km E.Ocozocaut la 820m. 4.VI.1990 H. & A. Howden;

at light [UASM]; 1 male: MEX. Chiapas,Parque Laguna Belgica 27-V-1987, D.A. Rider E. G. & T.J. Riley; collected at mercury vapor & blacklight [LSUC]; 1 male: MEX. Veracruz Rancho Clacotengo,ca.2-5km. n. Fortin de las Flores,1120m.,pasture in bromeliads 78B-32 December 21, 1978; MEXICAN EXP. 1978-1979 G.E.&K.E. Ball Collectors [UASM]. 1 male: Mexico, Rascón zw.SanLuisPotosi u.Tampico VIII.1911 C.A.Purpus S.V. [MNHB]. 1 female: Chiacaman, Vera Paz. Champion; B.C.A. Col. I.1 Coptodera unicolor, Chevr. [BMNH]. 1 female: BRITISH HONDURAS Cayo Dist. Augustine Pine Ridge Forest Station, u.v.light 3-VII-68. W.L.Hasse [FSCA]. 1 male: BRITISH HONDURAS Cayo Dist.Augustine Pine Ridge, u.v.light 4-VII-1968 W.L.Hasse [FSCA]. 1 male and 1 female: BR.HONDURAS Belize District WesternHwy Mi 15 08 Jun 1968 Light:UV, trap; Hasse,W.L. Collector [FSCA]. 1 male: HONDURAS., Dept.Comajagua, Rancho Chiquito Km.62,UV-light, 29 May 1964; F.S. Blanton, A.B. Broce, R.E. Woodruff, Collectors [FSCA]. 3 males and 2 females: BELIZE:Cayo District Mountain Pine Ridge, Hidden Valley. 650- 700m. 89-00W,17-00N; 24 May 1990 Norton S. Adams, Linwood C. Dow Pine-oak savanna [CMNH]. 3 males: BELIZE:Cayo District Mountain Pine Ridge, Hidden Valley. 650- 700m. 89-00W,17-00N; 22-29 May 1990 Norton S. Adams, Linwood C. Dow pine-oak savanna [CMNH].

Type locality.-- Guadalupe Canyon, Cochise County, state of Arizona, United States of America.

Derivation of specific epithet.-- From Medieval Latin *brunneous*, in allusion to the brown color of this species.

Recognition.-- This species is readily separated from the other species of the *C. aerata* group by a combination of the following three characters: brown color, antennomeres 3 and 4 darkened, and small sensory pits on the ventral surface of antennomeres 5-11 (Fig. 1B).

Description.-- Character states of the *C. aerata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head, pronotum and elytra rufo-brunneous to dark brunneous; lateral margin of elytron paler or not; antennae rufous, antennomeres 3 and 4 darkened (contrasting with antennomeres 2 and 5); mouthparts rufous to rufo-brunneous; appendages brunneous, femora paler basally. Ventral surface brunneous to dark brunneous; epipleuron paler medially.

Elytra. Interneurs impunctate.

Male genitalia. As in Figs. 34C-34D, median lobe with membranous portion short. Apical portion medium, flattened, in lateral aspect trianguloid, rather broad, in dorsal aspect trianguloid, broad; apex in lateral aspect narrowly rounded, in dorsal aspect broadly rounded. Internal sac spine A medium in size; spine group B absent; spine group C with three medium-small spines.

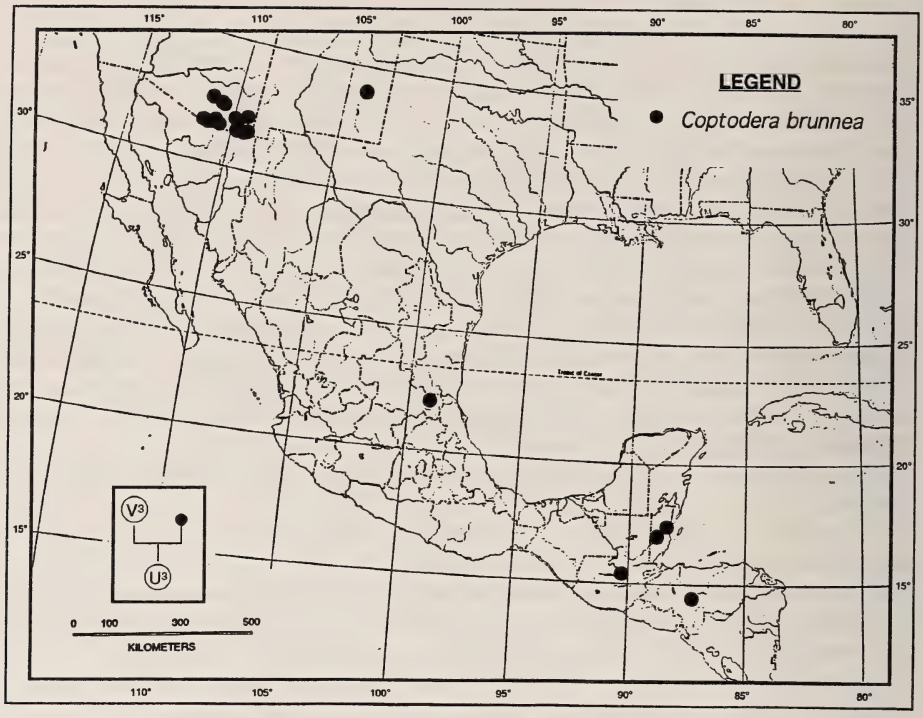
Notes about habitat.-- In Belize and Honduras specimens were taken at u-v light. In México, one specimen was taken at an altitude of 1120 m from bromeliads in a tree growing in a pasture; a second at mercury vapor and blacklight. In United States, specimens were taken at altitudes of 1191-1828 m; at blacklight; at mercury vapor lights; at light; and in bait traps.

Geographical distribution (Map 18).-- This species ranges from Nuclear Central America (Honduras and Belize) northward on the Gulf Versant of México to the southwestern United States.

Chorological affinities.-- The range of *C. brunnea* is overlapped completely by the range of its adelphotaxon, *C. nitidula* (Maps 17 and 18).

Phylogenetic relationships.-- See topic for *C. nitidula* above, the adelphotaxon of *C. brunnea*.

Material examined.-- Type material only; see above for details.



MAP 18. Geographical distribution of *Coptodera brunnea*, new species. Inset indicates phylogenetic relationship of species as illustrated in Fig. 36.

Coptodera aerata Dejean
Figs. 1H, 6D, 6H, 12M-12P, 34E & 34F; Map 19

Coptodera aerata Dejean 1825: 277. Type material: LECTOTYPE (here selected) male, labelled: TYPE (red paper); aerata in Amer bor (Dejean's handwriting on green paper); Ex Musaeo Chaudoir (red print); LECTO- TYPE (disc with purple border); LECTOTYPE Coptodera aerata Dej. det. George E. Ball '72; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: United States.-- LeConte 1848: 196.-- Horn 1881: t. 8, f. 84.-- 1882: 131.-- Blatchley 1910: 149.-- Ball 1960: 158.

Coptodera viridipennis Gory 1833: 194. Type material: HOLOTYPE male, labelled: viridipennis LeConte Gory; Museum Paris ex Coll R. Oberthür (light green paper) [MNHP]. Type area: United States (incorrectly given in the original description as Java).-- Chaudoir 1869: 179.

Coptodera viridipennis LeConte 1848: 196. Type material: LECTOTYPE (here selected) male, labelled: orange disc (south-eastern United States); var. viridipennis LeC. [MCZ]. Type locality: Alabama, United States.-- Horn 1882: 160.

Coptodera ruficornis Chaudoir 1869: 179. Type material: LECTOTYPE (here selected) female, labelled: LECTO (red paper); TYPE (red paper); ruficornis Chaud (handwritten); Louisiane Guex (handwritten); Ex Musaeo Chaudoir (red print); LECTOTYPE Coptodera ruficornis Chaud det. George E. Ball '87; Museum Paris ex Coll R. Oberthür (light green paper)[MNHP]. Type locality: Louisiana, United States.-- Horn 1882: 160.

Note about synonymy.-- We confirm the synonymy by Chaudoir and Horn, noted above, based on the study of type material.

Notes about type material.-- Chaudoir (1869: 179) listed *C. viridipennis* Gory as a junior synonym of *C. aerata* followed by a reference to LeConte's publication. Gory's collection of Carabidae was acquired by Chaudoir in 1852 (Basilewsky 1983: 465). In the MNHP there is a Chaudoir specimen bearing a label "viridipennis LeConte Gory". We believe that this specimen is Gory's type, and was labelled by Chaudoir indicating that *C. viridipennis* of both LeConte and Gory was the same species. Gory's material must have been incorrectly labelled as this species is known only from United States.

Notes about nomenclature.-- Although the name *Coptodera viridipennis* LeConte is a junior primary homonym of *C. viridipennis* Gory, according to the International Code of Zoological Nomenclature (Third Edition, Article 60), a replacement name is not required for *C. viridipennis* LeConte because this name is a junior subjective synonym.

Description.-- Character states of the *C. aerata* group and the following. See Tables II-VII for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum brunneous to rufo-piceous with faint green lustre; elytra metallic green to blue-green, at times aeneous laterally; antennae, mouthparts and appendages brunneous. Ventral surface brunneous to dark brunneous.

Fixed setae. Disc of elytron with three setigerous punctures.

Mouthparts. Labrum as in Fig. 1H; labium as in Figs. 6D & 6H.

Elytra. Interneurs impunctate.

Male genitalia. As in Figs. 34E-34F, median lobe with membranous portion medium-short. Apical portion medium-long, in lateral aspect trianguloid, slender, tapered gradually toward apex, in dorsal aspect trianguloid but constricted preapically; apex in lateral aspect narrowly rounded, in dorsal aspect sub-truncate. Internal sac spine A small; spine group B with two small spines; spine group C with two small spines.

Ovipositor. Stylomere 2 as in Figs. 12M-12P.

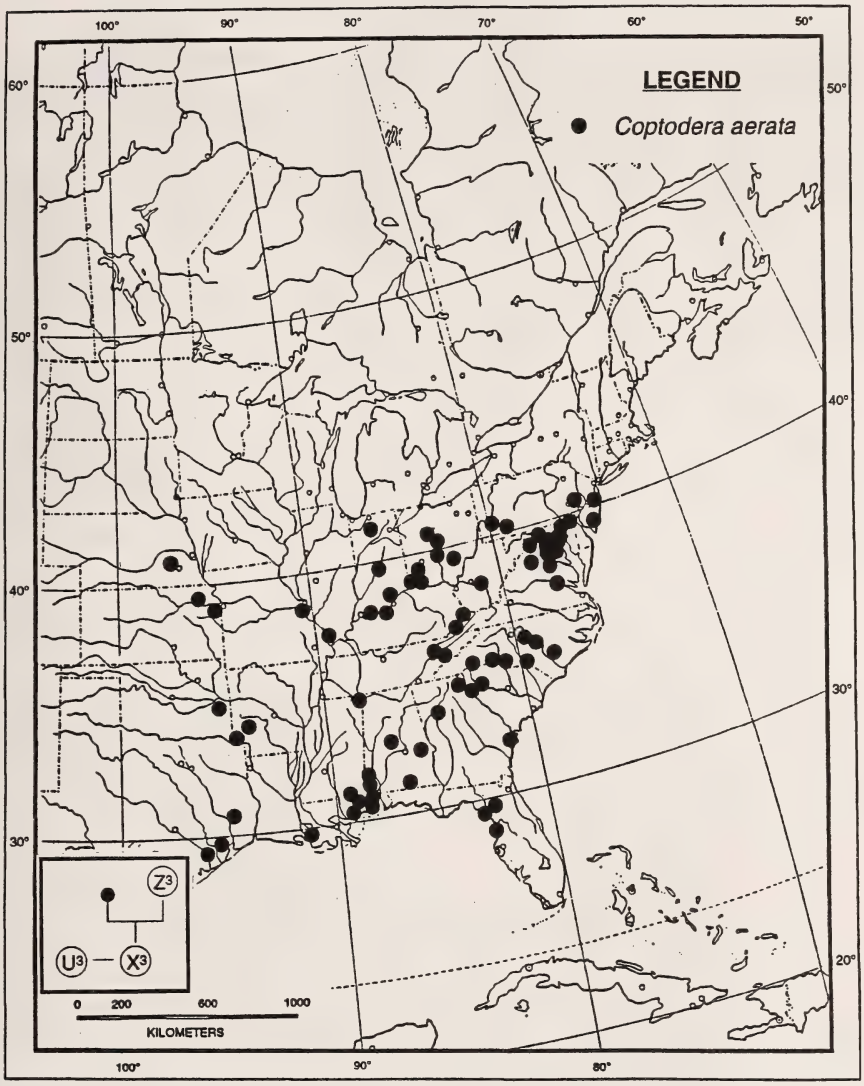
Notes about habitat.-- Specimens were taken at altitudes of 30-762 m. Specimens were taken at light, both white and uv; under bark; under cyprus and oak bark; on dead oak and beech; by sweeping oak; in garbage; in a light trap at a tobacco warehouse; and by beating in upland and lowland forest.

Geographical distribution (Map 19).-- This species is found in the United States only, and probably only in the forested areas of the east, and the gallery forests of the Mississippi drainage basin, in the west. We believe the Montana specimen is mislabelled and the Arizona specimen is probably mislabelled.

Chorological affinities.-- The range of *C. aerata* is separated widely from that of its adelphotaxon, *C. waytkowskii* (Maps 19 and 20). In fact, *C. aerata* is isolated geographically from all other known species of *Coptodera*.

Phylogenetic relationships (Fig. 36).-- Based on the derived feature of reduced spines in the internal sac (Figs. 34E & 34F; cf. Fig. 34G & 34H), this species and *C. waytkowskii* are postulated to be adelphotaxa.

Material examined.-- A total of 490 specimens, including types, were examined. Non-type material was seen from the following localities:
U.S.A. Alabama. Dale Co. Ft. Rucker Mil. Res. (RHTC); Jefferson Co. Birmingham (FMNH); Lee Co. Auburn (USNM); Mobile Co. 18.2 km e Citronelle (AMNH); Magazine Pt. (CAS); Mobile (MCZ); Mt. Vernon (CAS); **Arizona**. Santa Cruz Co. Peña Blanca (AMNH); **Arkansas**. Franklin Co. Ozark Natl. For., Gray's Picnic Area on FSR 1003 (DAPC); Garland Co. Hot Springs (CUIC)(MCZ); Hempstead Co. Hope (MCZ); Pulaski Co. South West (AMNH); **Delaware**. New Castle Co. Newark (UASM); **D.C.** (CMNH)(USNM); Rock Creek (USNM); Rock Creek Pk. (USNM); Rock Creek Valley (USNM); Washington (CUIC)(USNM); **Florida**. Alachua Co. (FSCA); Gainesville (FSCA); Dixie Co. Pine Landing (UASM); Hernando Co. 9.7 km w Brooksville (FMNH); Liberty Co. Torreya St. Pk. (RHTC); **Georgia**. (IZWP); Atlanta (FMNH); **Illinois**. (CMNH); Alexander Co. Olive Branch (CAS)(FMNH); **Indiana**. Crawford Co. Grantsburg (FSCA); Jefferson Co. Madison (FSCA); Marion Co. Indianapolis (FSCA); St. Joseph Co. Pine (FMNH); **Kansas**. Shawnee Co. Topeka (USNM); Wyandotte Co. Argentine (AMNH); **Kentucky**. (AMNH)(CAS)(CMNH)(CUIC)(MCZ)(OSUC)(USNM); Christian Co. 8 km w Hopkinsville (DAPC); Henderson Co. Henderson (MZUM; Rowan Co. Morehead (CNC); **Louisiana**. St. Mary Co. Morgan City (MCZ); **Maryland**. (BMNH)(CMNH); Baltimore (CAS)(IZWP)(USNM) (ZSMM); Anne Arundel Co. Odenton (CUIC); Baltimore Co. Gunpowder (USNM); Calvert Co. Flag Ponds Nature Park (USNM); Harford Co. Edgewood (USNM); Montgomery Co. Colesville (MCZ); Glen Echo (USNM); Takoma Park (CAS)(DHK)(CNC); Prince Georges Co. Beltsville (FSCA)(USNM); Bladensburg (USNM); Branchville (USNM); College Park (FSCA); **Michigan** Monroe Co. Toledo Beach (USNM); **Mississippi**. George Co. Lucedale (CUIC); Harrison Co. Gulfport (CUIC); Perry Co. New Augusta (CUIC); Smith Co. 3.7 km e Polkville (RHTC); County? Lakesville (CUIC); County? R.F. Laird Agr. Co. (CUIC); **Missouri**. St. Louis (CAS)(MCZ)(USNM); **Montana**. Gallatin Co. West Yellowstone (CAS); **Nebraska**. Lancaster Co. Malcolm (FMNH); **New Jersey**. Camden Co. Grenloch (OSUC); Cape May Co. Ocean City (AMNH); Monmouth Co. Englishtown (FMNH); **North Carolina**. (MCZ); Buncombe Co. Weaverville (USNM); Catawba Co. Hog Hill (CMNH); Cleveland Co. Shelby (CNC); Duplin Co. West (CMNH); Durham Co. Durham (CDAE); Mecklenburg Co. Charlotte (CNC); Moore Co. Southern Pines (CAS); Wake Co. Raleigh (BMNH)(CNC); **Ohio**. (AMNH)(CAS)(MCZ)(MPMM)(USNM); Clermont Co. (AMNH); Clinton Co. (OSUC); Crawford Co. Plankton (CAS); Delaware Co. (OSUC); Franklin Co. Columbus (OSUC); Hamilton Co. Cincinnatti (BMNH)(CAS)(MCZ)(USNM); Hocking Co. (OSUC); **Oklahoma**. Latimer Co. (FSCA); 8 km w Red Oak (FSCA)(UASM); **Pennsylvania**. (OSUC); Allegheny Co. (CMNH)(CUIC); Pittsburgh (CMNH); Bucks Co. Tinicum Is. (USNM); Delaware Co. Broomall (AMNH); Chadds Ford (JEWC); Lansdowne (AMNH); Upper Darby (USNM); Westmoreland Co. Jeanette (CMNH); **South Carolina**. Beaufort Co. (USNM); Oconee Co. 8 km n Oconee St. Pk., Sumter National For. (DHK); Pickens Co. Clemson College (USNM); Spartanburg Co. Camp Croft (FMNH); **Tennessee**. (MCZ); Davidson Co. Nashville (MCZ); Knox Co. Knoxville (CNC); Obion Co. Reelfoot Lake, Horse Island (DAPC); Sevier Co. Gatlinburg (CNC); **Texas**. (BMNH)(MCZ); Colorado Co. Columbus (USNM); Gonzales Co. Palmetto State Park (CMNH); Harris Co. Houston (USNM); Nacogdoches Co. Nacogdoches (CNC); **Virginia**. Falls Church (CAS)(USNM); Richmond (USNM); Alex Co. (MCZ)(USNM); Fairfax Co. (CMNH); Gt. Falls (USNM); Mt. Vernon (CAS)(USNM); Fauquier Co. Belvoir (USNM); Lee Co. Jone's Creek (MCZ)(USNM); Pennington Gap (USNM); Loudoun Co. Lucketts (USNM); Nelson Co. (USNM); Shipman (USNM); Prince William Co. Occoquan (USNM); Not located "Ash Grove" (CUIC) and "Veitch" (USNM). **West Virginia**. Nicholas Co. nr. Summersville (CMNH).



MAP 19. Geographical distribution of *Coptodera aerata* Dejean. Inset indicates phylogenetic relationship of species as illustrated in Fig. 36.

No or mixed labels (BMNH)(CAS)(IZWP)(MCZ). Collections in all months of the year except for March and December.

Coptodera waytkowskii Liebke
Figs. 33D, 34G & 34H; Map 20

Coptodera waytkowskii Liebke 1951: 243. Type material: HOLOTYPE, male, labelled: PERU Satipo, x-xii 1935, F. Waytkowski, B.M. 1936-732; Sammlung, M. Liebke (light green paper); Type (pink paper); Coptodera waytkowskii Lbk. M. Liebke determ. Type; Inst. Zool. P.A.N. Warszawa 31/54 [IZWP]. Type locality: Satipo, Junín dept., Peru.

Description.-- Character states of the *C. aerata* group and the following. See Tables II, IV, and VI for data about variation in standardized body length, and in values for ratios Hw/Pw and Pw/Pl.

Color. Head rufo-testaceous to rufo-brunneous; pronotum lighter, testaceous to rufo-testaceous; elytra brunneo-testaceous to brunneous with faint to moderate aeneous lustre and testaceous preapical markings, lateral margin testaceous to rufo-testaceous; mouthparts, antennae, and legs testaceous to rufo-testaceous. Ventral surface testaceous to brunneous.

Head. Fine setae between posterior pair of supraorbital setae.

Elytra (Fig. 33D). Interneurs finely punctate.

Male genitalia. As in Figs. 34G-34H, median lobe with membranous portion medium-short. Apical portion medium-short, flattened, in lateral aspect trianguloid, moderately broad, tapered gradually toward apex, in dorsal aspect broad, hardly tapered; apex in lateral aspect narrowly rounded, in dorsal aspect broadly rounded. Internal sac spine A small; spine group B with one small spine; spine group C with two small spines.

Notes about habitat.-- None available.

Geographical distribution (Map 20).-- This species is known only from the Amazon Basin of South America, in eastern Brazil and eastern Peru.

Chorological affinities and phylogenetic relationships (Fig. 36).-- See these topics for *C. aerata* above, the postulated adelphotaxon of *C. waytkowskii*.

Material examined.-- We examined 3 specimens, including the holotype, and saw non-type material from the following localities:
BRAZIL Para. (CMNH);
PERU Junín. Satipo (IZWP);

Coptodera erwini, new species
Fig. 33E; Map 20

Type material.-- HOLOTYPE, female labelled: PERU: MADRE DE DIOS Pakitza, Zone 02 16Sept88 T.L.Erwin & B.D. Farrell Colls 12°07'S 70°58'W; Insecticidal Fog Canopy/Celtis BIOLAT 02131512; BIOLAT/COLE 000008471 [USNM].

Type locality.-- Pakitza, department of Madre de Dios, Peru.

Derivation of specific epithet.-- This is the Latinized surname of Terry L. Erwin, who has collected many fine carabids from the forest canopy, including the type specimen of this species, using his fogging technique. He has also collected many specimens of other *Coptodera* species in Central and South America.

Description.-- Character states of the *C. aerata* group and the following. See Tables III, V and VII for data about standardized body length, and ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum rufo-testaceous; elytra rufo-testaceous in basal half, dark brunneous in apical half; lateral margin of elytron rufo-testaceous; appendages, antennae and

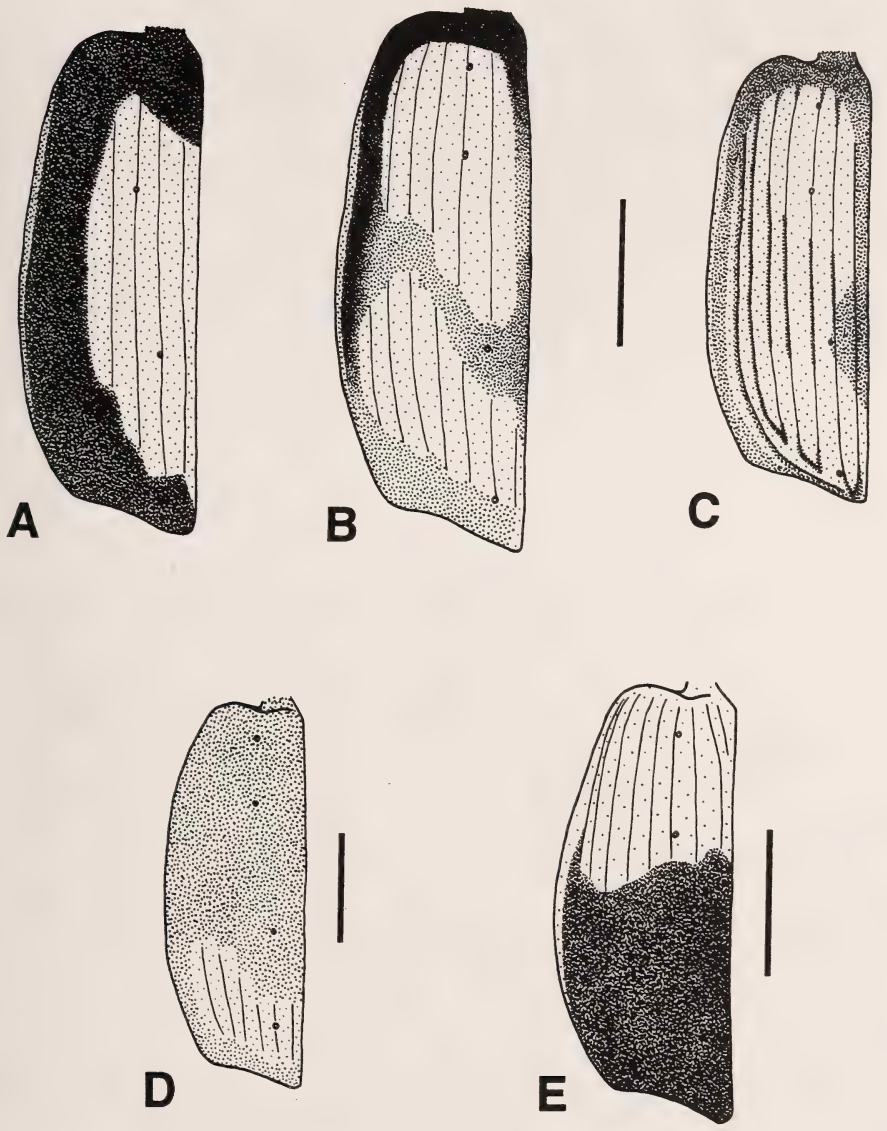


FIGURE 33. Line drawings of left elytron of *Coptodera aerata* group, dorsal aspect. Figs. A-C: *C. nitidula* (Buquet). Fig. D: *C. waytkowskii* Liebke. Fig. E. *C. erwini*, new species. Scale bars = 1 mm.

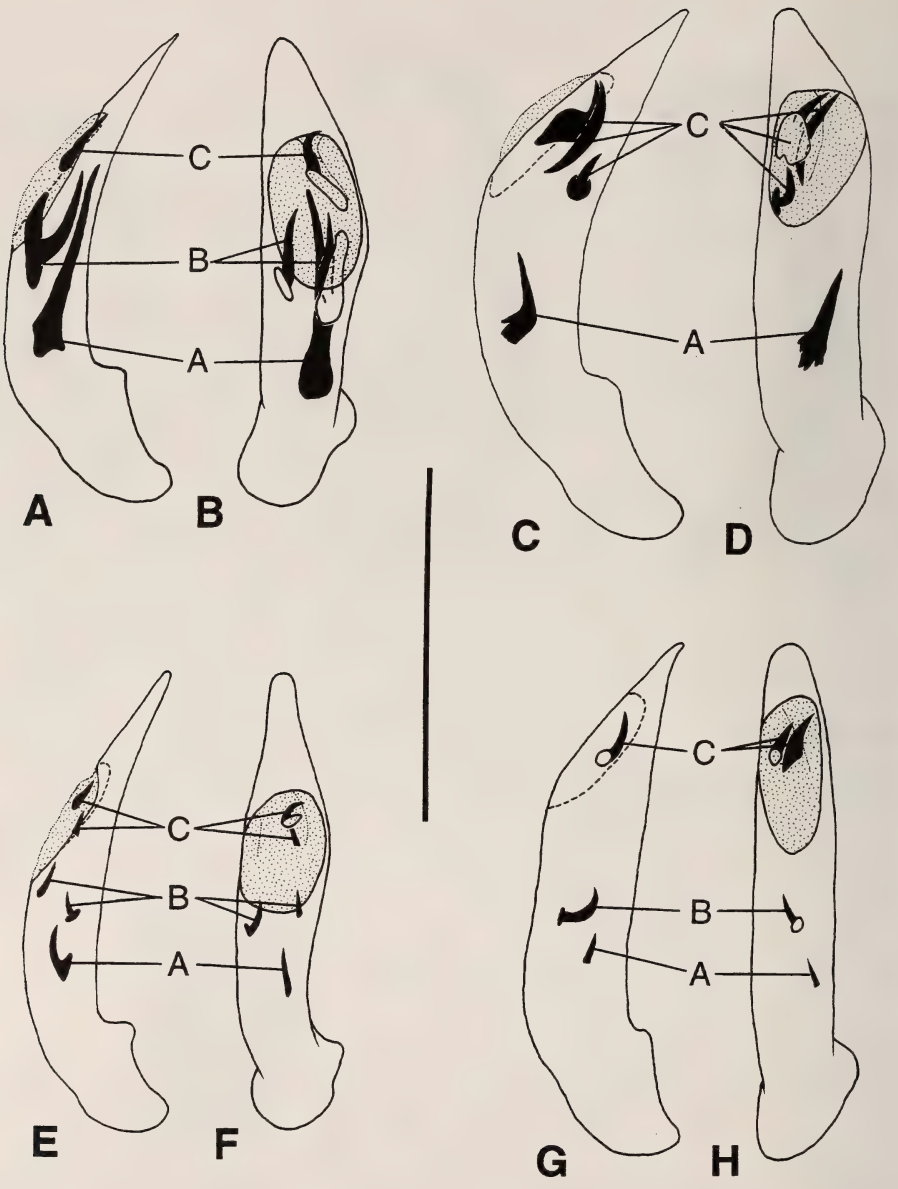
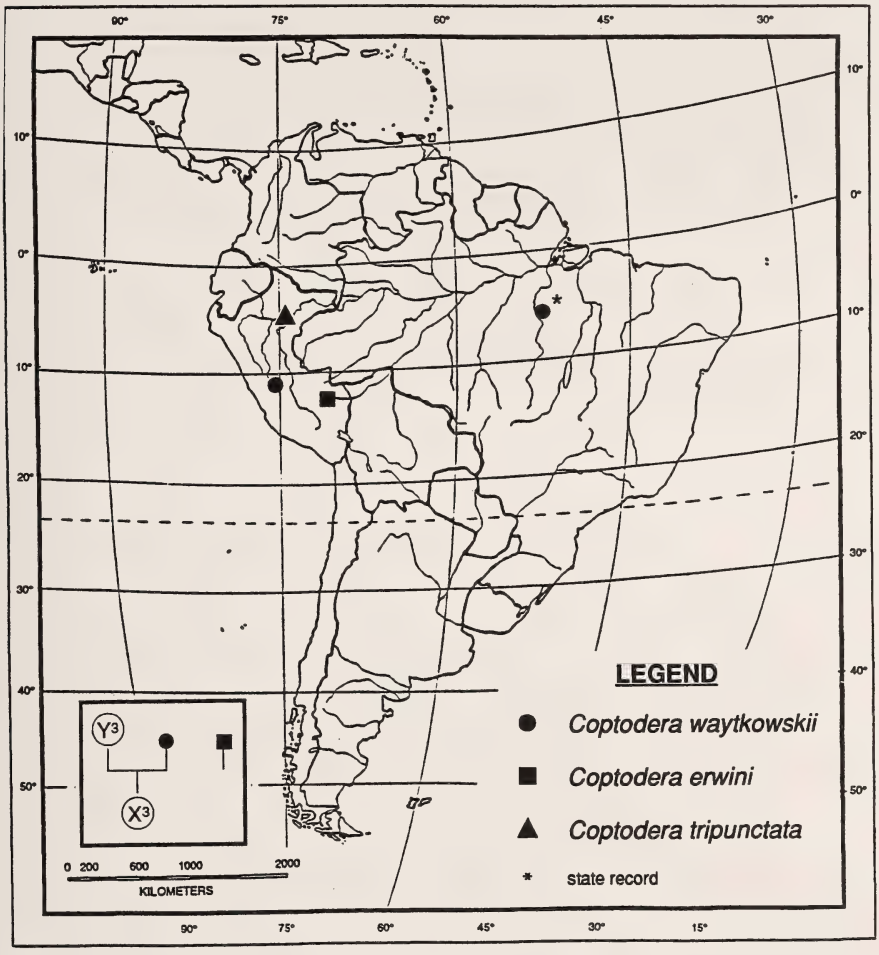


FIGURE 34. Line drawings of male genitalia of *Coptodera aerata* group. Figs. A, C, E & G left lateral aspect. Figs. B, D, F & H dorsal aspect. Figs. A-B: *C. nitidula* (Buquet). Figs. C-D: *C. brunnea*, new species. Figs. E-F: *C. aerata* Dejean. Figs. G-H: *C. waytkowskii* Liebke. Scale bars = 1 mm. Legend: A, spine A; B, spine B; C, spine C.



MAP 20. Geographical distribution of *Coptodera waytkowskii* Liebke, *C. erwini*, new species and *C. tripunctata*, new species. Inset indicates phylogenetic relationships of species as illustrated in Fig. 36.

mouthparts rufo-testaceous. Ventral surface of head and prothorax rufo-testaceous, mesepimeron and mesepisternum slightly darkened; metepisternum, metepimeron, metasternum and abdominal sterna rufo-piceous; metasternum slightly lightened medially (elytral epipleuron rufo-testaceous).

Elytra (Fig. 33E). Interneurs impunctate.

Male genitalia. Unknown.

Notes about habitat.-- The type specimen was taken from the canopy of *Celtis* L. by fogging with an insecticide.

Geographical distribution (Map 20).-- This species is known only from the type locality in southern Peru.

Chorological affinities.-- The type specimen of this species and specimens of *C. nitidula* were both collected at the same time at Pakitza, Madre de Dios, Peru.

Phylogenetic relationships (Fig. 36).-- The position of this species is unresolved due to the lack of a male specimen; it is tentatively placed at the end of the *C. aerata* group lineage.

Material examined.-- Type material only, see above for details.

Species *Incertae Sedis*

Coptodera deplanata Motschulsky 1864: 223. Type material: not located. Type area: Brazil.

No type specimen could be located, and the description is not clear as to whether or not this species is even a *Coptodera*.

Checklist of New World Species of *Coptodera*[1]

sallei group
- sallei, new name. Guatemala, México
  - *variegata* Chaudoir 1869: 168

elongata group
- elongata Putzeys 1845: 395. Costa Rica, Guatemala, México
- schaumi Chaudoir 1861: 123. Brazil, Colombia?, Costa Rica, Guatemala, Nicaragua, Panamá
  - *bifasciata* Schaum 1860: 191
- megalops Bates 1869: 77. Bolivia, Brazil, Colombia, Ecuador, Peru
  - *batesi* Chaudoir 1869: 172
  - *pertzeli* Liebke 1951: 242
  - *peruana* Liebke 1951: 243
- championi Bates 1883: 180. Colombia, Panamá, Nicaragua
- apicalis new species. Colombia, Ecuador

aurata group
- xanthopleura Bates 1891: 270. México
- aurata Chevrolat 1835: No. 162. México, Guatemala
- viridis new species. México

depressa group
- depressa Dejean 1831: 393. Argentina, Brazil, Colombia, Paraguay, Peru
  - *undulata* Perty 1830: 5
  - *plaumanni* Liebke 1939: 127
- versicolor Bates 1869: 76. Bolivia, Brazil, Colombia Ecuador, Peru, Venezuela
  - *affinis* Chaudoir 1869: 168

[1] Synonyms in italics

transversa group
dromioides (Bates) 1869: 79. Brazil, French Guiana
corticalis Chaudoir 1869: 207
nigrosignata (Chaudoir) 1869: 206. Brazil
fulminans (Bates) 1869: 78. Brazil
nigrostriata (Reiche) 1843: 179. Bolivia, Brazil, Colombia, Peru, Venezuela
multiguttata Putzeys 1845: 377
variegata Chaudoir 1848: 117
pallida Bates 1869: 78
lineata (Bates) 1883: 184. Costa Rica, Guatemala, México, Nicaragua, Panamá
stockwelli, new species. Panamá
transversa (Reiche) 1843: 179. Bolivia, Brazil, Colombia, Costa Rica, Guatemala, México, Panamá
atriceps Bates 1869: 78
picturata Chaudoir 1869: 205
undulata Chaudoir 1869: 206
sigillata, new species. Brazil
squiresi (Chaudoir) 1869: 201. Brazil
festiva group
sahlbergi Chaudoir 1869: 181. Argentina, Bolivia, Brazil, Paraguay
discicollis Chaudoir 1869: 181.
relucens Bates 1869: 73. Brazil
lebioides Bates 1869: 74
rotundipennis Chaudoir 1869:182
poecila Bates 1883: 183. Panamá
pakitza, new species. Peru
festiva Dejean 1825: 274. Brazil, Costa Rica, Cuba, Guatemala, Haiti, Jamaica, México, Panamá
chloris Bates 1883: 182
chalcoptera Chaudoir 1869: 184
foveolata new species. México
nigroviridis new species. México
rufescens Buquet 1835: 617. French Guiana, Brazil
luteopicta Chaudoir 1850: 363
teutonica, new species. Brazil
aeneorufa group
aeneorufa Bates 1869: 76. Bolivia, Brazil, Ecuador, Surinam
bifasciata group
bifasciata Putzeys 1845: 394. Bolivia, Brazil, Venezuela
tripartita Chaudoir 1869: 180. Brazil
cupreotincta Bates 1869: 73. Bolivia, Brazil, Costa Rica, México, Nicaragua, Panamá, Peru
tesselata Chaudoir 1869: 199
amazonica Chaudoir 1869: 200
braziliensis new species. Brazil
emarginata group
chalcites Bates 1869: 75. Brazil, Ecuador, Peru
aeneocuprea Chaudoir 1869: 177

emarginata Dejean 1825: 276. Brazil
aenea Buquet 1834: 673
acutipennis (Buquet) 1834: 674. Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guatemala, México, Nicaragua, Panamá, Peru, Trinidad
spinipennis Bates 1869: 75
scintillans Bates 1878: 604

picea group
picea Dejean 1826: 458. Belize, Bolivia, Brazil, Colombia, Cuba, Guatemala, Guyana, Honduras, México, Nicaragua, Panamá, Paraguay, Peru, Surinam, Trinidad, Venezuela, United States
velox Gory 1833: 195
rufula Buquet 1834: 680
unicolor Chevrolat 1834: No. [40]
obscura Laporte 1834: 51

aerata group
nitidula (Buquet) 1834: 677. Argentina, Bolivia, Brazil, Costa Rica, Ecuador, French Guiana, Guatemala, Guyana, México, Nicaragua, Panamá, Paraguay, Peru, Surinam, United States
triangularis Buquet 1834: 678.
luculenta Erichson 1847: 69
debilis Bates 1869: 76
flavodisca Chaudoir 1869: 187.
nubiculosa Chaudoir 1869: 186.
flavodisca immaculipennis Bates 1883: 182.
brunnea new species. Belize, México, United States
aerata Dejean 1825: 277. United States
viridipennis Gory 1833: 194
viridipennis LeConte 1848: 196
ruficornis Chaudoir 1869: 179
waytkowskii Liebke 1951: 243. Brazil, Peru
erwini, news species. Peru

tripunctata, new species. Peru

species *incertae sedis*
deplanata Motschulsky 1864: 223. Brazil

Misplaced Species

Eucalyptocola marcida Blackburn 1903: 91. HOLOTYPE female, glued to card on which is written T. Nels.V. 7/89 ("T." in black print, remainder in red print); Type (disc ringed with red); Blackburn Coll 1910-236; Eucalyptocola marcida Blackb (handwritten); Coptodera marcida Blackb /87 det. George E. Ball; Microlestodedes marcida Blackbn det B.P. Moore 1987 [BMNH].-- Sloane 1907: 376,377.

Sloane (1907) transferred this species to the genus *Coptodera*. At the authors' request, B.P. Moore confirmed that the type specimen in question was not a member of *Coptodera*, and identified it as a member of *Microlestodes* Baehr.

Coptodera philippinensis Jedlička 1935: 116. HOLOTYPE male, glued to card, and labelled: Type (disc ringed with red); Philippine Is. Coll. Bottcher. B.M. 1929-201; Coptodera philippinen- type sis sp.n. Det.ING.JEDLIČKA (first three lines handwritten; salmon-colored paper); 217 (handwritten); Coptodera philippi -ensis ♂ Jedl. det. George E. Ball /87 [BMNH].

This specimen is a member of the metallicine genus *Anchista* Nietner. Accordingly, it is transferred herewith.

Coptodera robusta Bates 1884: 296. HOLOTYPE female, labelled: Type H.T. (disc ringed with red); Costa Rica Van Patten.; B.C.A. Col. I.1. Coptodera robusta Bates; Coptodera robusta Bates (in Bates' handwriting); HOLOTYPE ♀ Coptodera robustus Bts. By Erwin '76 [BMNH].

This specimen is a member of the subgenus *Phloeotherates* Bates, in the genus *Stenognathus* Chaudoir. Accordingly, it is transferred, herewith.

Coptodera polygona Bates 1869: 72. LECTOTYPE female, here selected, labelled: Ega; polygona Bates; Lelis bifasciata Chaud; Ex Musaeo H.W. Bates 1892; LECTO- TYPE (disc ringed with purple); LECTOTYPE Coptodera polygona Bts. det. George E. Ball '72 [MNHP].

This specimen is a member of the genus *Lelis* Chaudoir, and is transferred accordingly, herewith.

Coptodera latipennis Bates 1869: 72. HOLOTYPE female, labelled: S. Paulo Amaz (handwritten); latipennis Bates (handwritten); Ex Musaeo H.W. Bates 1892; HOLO (red paper); TYPE (red paper); latipennis Bates Ent M. M. July 1869; Museum Paris ex Coll R. Oberthür (light green paper); HOLOTYPE Coptodera latipennis Bates det. George E. Ball '72 [MNHP].

This specimen is a member of the genus *Lelis* Chaudoir, and is transferred accordingly, herewith.

Coptodera rutila Bates 1869: 75. LECTOTYPE female, labelled: Ega; rutila Bates; 702 (blue paper); Lelis viridipennis Chaud; TYPE (red paper); LECTO TYPE (disc with purple border); LECTOTYPE Coptodera rutila Bates det. George E. Ball '72 [MNHP].

This specimen is a member of the genus *Lelis* Chaudoir, and is transferred accordingly, herewith.

Species Names With New Status

Coptodera chaudoiri Andrewes, NEW STATUS

Coptodera transversa Schmidt-Goebel 1846: 54 (*nec* Reiche). Type material not seen. Type area: Burma.

Coptodera bicincta Chaudoir 1869: 187 (*nec* Hope). Type material: not seen. Type area: Hong Kong.

Coptodera interrupta Bates 1892: 411 (*nec* Schmidt-Goebel). Type material: not seen. Type area: Burma.

Coptodera chaudoiri Andrewes 1919: 179. Type material: not seen. Type area: Hong Kong.

Coptodera transversa Schmidt-Goebel is a junior primary homonym of *C. transvera* Reiche 1843: 179. *C. bicincta* Chaudoir (1869: 187) is not available, as it is a junior primary homonym of *C. bicincta* Hope (1845: 15) which is presently in *Somotrichus* Seidlitz. *C. interrupta* Bates (1892: 411) also is not available, as it is a junior primary homonym of *C. interrupta* Schmidt-Goebel (1846: 53). *Coptodera chaudoiri* Andrewes is the valid name for this species.

Coptodera fasciolata Macleay, NEW STATUS

Scopodes auratus Macleay 1871: 92 (*nec* Chevrolat). Type material: not seen [ANIC]. Type locality: Gayndah, Queensland, Australia.

Ectinochila tesselata Chaudoir 1883: 22 (*nec* Chaudoir 1869). Type material: not seen [MNHP]. Type area: Queensland, Australia

Scopodes fasciolatus Macleay 1887: 219. Type material: not seen [ANIC]. Type locality: Cairns, Queensland, Australia.

Sloane (1907: 381) synonymized the latter two names with *Coptodera aurata* Macleay (1871: 92) as the senior synonym. However, *C. aurata* Macleay is a junior primary homonym of *Coptodera aurata* Chevrolat (1835: 162). *Ectinochila tesselata* Chaudoir (1883: 22) normally would be the next available name, but it is a junior primary homonym of *Coptodera tesselatus* Chaudoir (1869: 199). The next available name, *Scopodes fasciolatus* Macleay (1887: 219), is not pre-occupied, and *Coptodera fasciolata* Macleay is the valid name for this species.

Ecological Considerations

This section is presented both to summarize information about aspects of the natural history of the New World species of *Coptodera*, and to provide a background for seeking the adaptive significance of the structural features of the species—a topic that is treated in the following sections. The evidence available is incomplete and anecdotal, consisting of rather casual or standard observations made and recorded in the course of collection of specimens.

All known species of *Coptodera* are forest inhabitants, with most species confined to the tropics between sea level and 2300 m altitude, and most species associated directly, and evidently for their entire lives, with trees. Erwin (1979b) classifies their habitat as "tree trunks and limbs" (p. 560), and as "logs, surface" (p. 584). Evidently, adults (and probably larvae) are predators on arthropods that live under bark or on standing or fallen tree trunks and branches (Bates 1869: 69).

Collection records, for specimens representing seven species groups at u-v light traps, provide evidence that adults fly, and that they are night-active. Adults of all of the New World species, in fact, are macropterous, with body proportions appropriate for flight (*i.e.*, elytra about 60 percent of the total length of body [cf. Frontispiece]).

Additional evidence for nocturnal activity is direct observation (by the authors and several colleagues) of adults of various species being seen at night on logs and at fruitfalls.

Association of some species (*Coptodera acutipennis* and *C. festiva*) with fruitfalls in tropical forest shows that foraging by adults is not confined to the vegetative parts of plants. In fact, adults of *C. acutipennis* have been taken principally at fruitfalls (seven collections), and only on the ground (excluding captures at light traps).

Local distribution of *Coptodera* seems to be patchy, and a correlate of trees in a suitable state of decomposition (*i.e.*, with bark loosened to some extent), or a correlate of occurrence and location of fruitfalls. Probably the under-bark habitats provide the resources required for only a single generation to be produced at each site. Thus, maintenance of dispersal ability among adults would be essential, and hence natural selection would favor the maintenance of flight capability.

Probably fruitfalls are only sources for feeding by adults, the latter eating maggots and other small saprophagous animals that are attracted to the fruit. Exploitation of fruit falls, because of their disjunct occurrence, would be achieved most readily by insects with flight ability.

TABLE XI. Sympatric assemblages of *Coptodera* species in the Neotropical Region.

Locality	Site	Species
MEX. Veracruz, 4 km W. Sontecomapan, 30 m IV.3-16.1966	Lowland evergreen forest, under bark	*elongata*, *aurata*, and *lineata*
SAME	SAME	*elongata*, *lineata*, *transversa*, and *picea*
MEX. Chiapas, 7.4 km N. Frontera-Comalapa, 732 m IX.2.1967	SAME	*xanthopleura*, *aurata*, and *cupreotincta*
MEX. Oaxaca, Rte. 175, 9 km S.Valle Nacional, 660 m VII.30.1972	Montane evergreen forest, under bark (of single fallen log)	*elongata*, *aurata*, and *cupreotincta*
PAN. Canal Zone, nr. sea level V- VII	Lowland evergreen forest, on logs and under bark	*championi*, *transversa*, *stockwelli*, *cupreotincta*, and *nitidula*
PAN. C.Z., Madden Dam for., nr. sea level VI.30.1972	Lowland evergreen forest, on logs	*championi*, *stockwelli*, and *cupreotincta*
PERU. Madre de Dios Pakitza 10°55'S, 71°35'W IX.10.1989	Lowland evergreen forest, running on logs	*megalops*, *versicolor*, and *chalcites*
SAME, but: 12°07'S, 70°58'W X.29-XI.01.1990	SAME	*aeneorufa*, *pakitza*, and *cupreotincta*

Among the species of *Coptodera*, requirements for life seem to overlap broadly, as indicated by occurrence of several species in the same habitats at the same time of year. The evidence for co-occurrence is presented in Table XI. Co-occurrence provides the potential for competition and genetic exchange among related species. No evidence is available for either of these phenomena in *Coptodera*.

Evolutionary Considerations

In this section, a reconstructed phylogeny is presented, based on analysis of structural features of *Coptodera* and its putative relatives. The resulting system of hypotheses is combined with an analysis of geographical distribution to provide an outline of the geographical history of the genus in the New World.

Reconstructed phylogeny

Methods.-- Our general approach to phylogenetic reconstruction, the "qualitative Hennigian method", is described in a passage by Saether (1990: 107) that also contrasts this method with the presently more widely used methods of quantitative phyletics or neocladistics: "In the qualitative Hennigian method, the parsimony criterion is used when choosing among alternative hypotheses of explanation of single character distribution. The selection and interpretation equals the cladogenetic analysis [or the search for adelphotaxa]. In neocladistic methods the parsimony criterion is used to find the tree implying the fewest evolutionary gains and losses with the fewest lines. The explanation of characters enters as an afterthought".

In more detail, the phylogeny of *Coptodera* was reconstructed in part by character analysis, and in part by attempting to discover and rationalize in an evolutionary framework the various groupings that were discovered by taxonomic analysis. For example, we recognized groups based on color, genitalic form and armature (or lack of it) in the internal sac, lobing of the posterior margin of the pronotum, and overall size. We found that such groups could be organized into two complexes, based on a combination of number of setae (or setigerous punctures) in elytral interval 3, and notching of the middle tibiae of males. We sought evidence to support these groupings, and to determine the pattern of adelphotaxon relationships.

Detailed character analysis was by outgroup comparison for initial polarization of character states, as explained by Ross (1974: 151-156), Wiley (1981: 139-146), Watrous and Wheeler (1981), and Maddison *et al.* (1984). We used also group trends, as explained by Ross (1974: 156). The direction of evolution of other characters was determined after a general pattern was perceived, by examining the pattern of distribution of states on a preliminary reconstruction of the phylogeny (a method designated character correlation by Hennig [1966] and by Ekis [1977], and the "functional outgroup/functional ingroup" method of Watrous and Wheeler [1981]. See also Ball and Maddison [1987: 258-259]). Characters were not weighted formally, but the features of the male genitalia and mandibles were analyzed in considerable detail.

Autapotypic and synapotypic character states are indicated in Table XII and in Figs. 35 and 36 by number, and are sequenced by letters and superscript numbers and letters. Postulated losses and reductions are indicated by a superscript minus sign. For characters with two or more apotypic states, each is designated by a different lower case letter, if each was postulated to be derived separately from the plesiotypic condition, thus forming a branched transformation series. If the apotypic states were postulated to form an unbranched transformation series, each state was labelled with the same letter but with a different number, implying direction of change (*i.e.*, a1, a2, a3). Character states postulated to represent reversals are indicated by a superscript "R". Stages in reversal were indicated by a number associated with superscript "R".

States of characters 12 and 28 were designated by their group-specific patterns. Group or lineage membership was indicated by a lower case letter.

For characters 13, 16, 46, 47, and 48, the variation pattern was so erratic that it was impossible to group them *a priori* in transformation series. Accordingly, apotypic states were designated simply by positive and negative numbers, indicating postulated distance and direction from the plesiotypic condition.

Other methods of phylogenetic analysis.-- See Appendix B for a synopsis of results of a numerical cladistic treatment of the data in Table XII.

Taxa studied.-- We examined representatives of: *Somotrichus unifasciatus* Dejean, and several species of *Pericalus* Macleay: *figuratus* Chaudoir, *undatus* Chaudoir, *signatus* Jedlička, *levifrons* Heller, *ornatus* Schmidt-Göbel, *cicindeloides* MacLeay, *amplus* Andrewes, and *tetrastigma* Chaudoir. Because of extensive parallelism in structural features between members of *Coptodera*

and *Pericalus*, and because of extensive parallelism between Old World and New World assemblages of *Coptodera*, we used *Somotrichus* as functional outgroup. We regard this genus as representing the most primitive assemblage of the subtribe Pericalina because of details of stylomere 2 of the ovipositor, which lacks a pronounced basal lobe, has three ensiform setae (two lateral, one medial), and has a pair of nematiform setae each inserted in a single ventral preapical sensory pit (Ball and Shpeley 1983: 748, Figs. 2a-c [cf. Figs. 3a-7c]). Basilewsky (1984: 552-553) places the somotrichoid assemblage in a group of its own, separate from the Pericalina, an arrangement that is consistent with our postulate, as long as somotrichines and pericalines (*sensu* Basilewsky) are regarded as adelphotaxa of one another.

Monophyly of the New World species of *Coptodera*.-- Jeannel (1949: 924) designated the New World species as the only members of *Coptodera*, and included the Old World species of the complex in other genera. Although we do not accept that *Coptodera* is a New World precinctive genus, for the purposes of phylogenetic analysis and in the absence of evidence to the contrary, we proceed as if all of the New World species are derived from a common ancestor that itself was a New World resident.

Phylogenetic analysis of the male genitalia of *Coptodera*.-- This analysis was difficult because of the extensive variation of these structures, not only between species that are postulated on other grounds to be related, but within at least one species (*C. acutipennis*). Some features were analyzed easily for the species assemblage as a whole (position of the ostium, size of the membranous portion of the median lobe, presence or absence of armature of the internal sac, and spine groups of the internal sac), but other features had to be analyzed in terms of the species groups (aspects associated with form and shape, and details of pattern of spination). Thus, we recognize five basic types, based on their overall size and general appearance: the *elongata* type (designated by "e"), characteristic of the *C. sallei*, *elongata*, and *aurata* species groups; the *depressa* type ("d"), characteristic of the *C. depressa* group; the *transversa* type ("t"), characteristic of the *C. transversa* group; the *festiva* type ("f"), characteristic of the *C. festiva*, *aeneorufa*, *bifasciata*, and *emarginata* groups; the *picea* type ("p"), characteristic of *C. picea*; and the *aerata* type ("a"), characteristic of the *C. aerata* group. Details are provided below.

Phylogenetic designation of character states.-- Each character is listed by number in sequence of its appearance in the reconstructed phylogeny (Figs. 35 and 36). Below, for each character, we note character states and the basis for their designation as plesiotypic or apotypic. See Table XII for details of character state distribution.

Character 00. Legs, tarsal claws: plesiotypic, inner margins smooth; apotypic, inner margins pectinate. See also character 50. Basis for designation: outgroup comparison.

Character 01. Labium: seta on palpiger. Two states: plesiotypic, asetose; apotypic, palpiger with single long seta (Fig. 6A, p). Basis for designation: outgroup comparison.

Character 02. Mentum, tooth. Two states: plesiotypic, dentate; apotypic, 02[-], edentate (Figs. 6A-D). Basis for designation: outgroup comparison.

Character 03. Ovipositor, stylomere 2, nematiform setae. Three states: plesiotypic, setae relatively long; apotypic, setae short (Fig. 12H, ns); apotypic, 03[-], setae absent. Basis for designation: outgroup comparison.

Character 04. Stylomere 2, microspinules. Two states: plesiotypic, absent; apotypic, present. Basis for designation: outgroup comparison.

Character 05. Elytra, discal setigerous punctures. Two states: plesiotypic, non-foveate; apotypic, foveate. Basis for designation: outgroup comparison.

Character 06. Elytron, number of discal setae. Two states: plesiotypic, four; apotypic, 06[-], three. Basis for designation: outgroup comparison.

Character 07. Ovipositor, stylomere 2, position of ensiform setae. Two states: plesiotypic, setae on dorsal margin; apotypic, setae lateral (Fig. 12A). Basis for designation: outgroup comparison.

Character 08. Labrum, anterior margin. Two states: plesiotypic, smooth, or shallowly emarginate; apotypic, narrowly, deeply emarginate (Figs. 1C-D). Basis for designation: outgroup comparison.

Character 09. Median lobe, position of ostium. Five states: plesiotypic, pleuropic-left (Figs. 19A-D); apotypic, 09^{a1}, left pleuropic-catopic, more pleuropic than catopic (Figs. 14B-C); apotypic, 09^{a2}, left pleuropic-catopic, more catopic than pleuropic (Figs. 16A-J); apotypic, 09^{b1}, anopic (Figs. 34A-H), and pleuropic-right, 09^{b2} (Figs. 28E-F).

Outgroup comparison indicates the anopic position as plesiotypic. However, within the New World taxa of *Coptodera*, the anopic position characterizes only the generally derived *picea-aerata* lineage. Thus, character correlation suggests that the anopic position is derived. Expressed in another way, with the *C. aeneorufa* group (lineage D^3, Figs. 35 and 36) as functional outgroup for lineage E^3, the left pleuropic-catopic position is seen as plesiotypic. What is known about genitalic structure and character trends for carabids in general, however, leads us to believe that the catopic condition is likely to be an end-point rather than a beginning.

The pleuropic-right position of the ostium is confined to another moderately derived lineage (F^3, Figs. 35 and 36). This leaves pleuropic-left as the position of choice for the plesiotypic condition: it is characteristic of the less derived *C. depressa* and *transversa* groups of lineage R.

With pleuropic-left as plesiotypic, we postulate change of position of the ostium in two directions: a, toward catopic; and b, to anopic, then to pleuropic-right (Fig. 39).

Character 10. Dorsal surface, luster. Three states: plesiotypic, dull; apotypic, shining; apotypic, dull, R-. Basis for designation: outgroup comparison and character correlation (the reversal).

Character 11. Male genitalia, armature of the internal sac. Three states: plesiotypic, without armature; apotypic, 11^{a}, with patch of microspines (Figs. 14B-C); apotypic, 11^{b}, with assemblage of macrospines (see, for example, Figs. 24A-P). Character state b is analyzed in detail as characters 46, 47, and 48. Basis for designation: outgroup comparison.

Character 12. Male genitalia, form of the median lobe. Analysis is in terms of a general pattern of form. See figures.

The *elongata* form (Figs. 14B-C, 16A-J, and 17A-F). Median lobe short and thick, apical portion short overall, of various widths (12e). In lateral aspect, apical portion rather broad, tapered to narrowly rounded apex, $12e^{a1}$ (Figs. 14B, 16A and C); apotypic, apical portion narrowed, triangular, $12e^{a2-}$ (Fig. 16E); apotypic, apical portion narrowed, subulate, $12e^{a3-}$ (Figs. 17A, C and E); apotypic, apical portion shortened and widened, $12e^{a2+}$ (Figs. 16G and I).

Within this complex, *C. xanthopleura* has an unusually slender median lobe, which could be an ancestral form. However, because of character correlation, we believe that this form is secondary, and thus is derived. It is designated $12e^{R}$.

The *depressa* form (Figs. 18A-D). Median lobe slender, with apical portion slender, of moderate size. The only difference between the two species is in distribution of the extensive membranous area (12d).

The *transversa* form (Figs. 21A-P, 22A-B). Median lobe slender, elongate, with apices of varying sizes, designated as follows. Plesiotypic, gradually curved ventrally, apical portion short and tapered to a narrowly rounded apex (12t). Apotypic states of apical portion ($12t^{a1}$

Fig. 21A) and still longer and curved ($12t^{a2}$, Fig. 21G); and apical portion much shorter and broader ($12t^{b-}$, Figs. 21I, K, and 22A-B).

The median lobe of the *festiva* form is slender with the apical portion of various lengths. Based on character correlation and outgroup analysis (with the *depressa* group as functional outgroup, lineage S, Figs. 35 and 36), the apical portion of moderate length is postulated to be plesiotypic (12f, Figs. 24A-B, 24I-J, and 25A-B). There are three apotypic forms, characterized by increasing length of the apical portion: $12f^{a1}$,(Figs. 24E-F, 24K-L, 27A-B, 27E-F, and 28E-F); $12f^{a2}$, (Figs. Figs. 24C-D, O-P); $12f^{a3}$ (Figs. 27C-D, and 27G-H); and $12f^{a4}$ (long and spatulate, Figs. 24M-N). One apotypic form is postulated to be a reduction or loss, by shortening of the apical portion ($12f^{b-}$, Figs. 24G-H, and 28C-D); and one taxon, *C. acutipennis*, has states that extend from $12f^{a2}$ to $12f^{b-}$ (Figs. 29A-P, 30A-L, and 31A-B).

The *picea* form of median lobe (Figs. 32A-B) is slender, with a long apical portion and the apex curved at tip (12p).

The *aerata* form of median lobe is various in lateral aspect, and broader than usual in dorsal aspect, in those species with a prominent apical portion (*C. aerata*, *nitidula*, and *brunnea*, Figs. 34A-F). By character correlation (trends for reduction in spines of the internal sac and in size of the membranous portion of the median lobe) we postulate as plesiotypic (12a) the *aerata* type of median lobe, with moderately broad and fairly long apical portion. The *nitidula-brunnea* type is apotypic ($12a^{a}$) in the somewhat shortened and broadened apical portion. The median lobe of *C. aerata* is postulated to be apotypic ($12a^{bi-}$) by reduction in width of the apical portion in dorsal aspect, a trend carried to *C. waytkowskii*, with the apical portion shortened markedly ($12a^{b2-}$).

Character 13. Male genitalia, median lobe, extent of dorsal membranous area. Five states: plesiotypic, size moderate (as in Figs. 16C-F, and 17A-D); apotypic, larger, 13^{1} (Figs. 19A-D); and smaller, 13^{1-} and 13^{2-} (Figs. 21E-H, and 22A-B); and reversal to moderate size, 13^{R-} (Fig. 21C-D). Basis for designation: outgroup comparison.

Character 14. Pronotum, lateral margins. Three states: plesiotypic, narrow; apotypic, wide; apotypic, narrow, 14^{R-}, reversal, loss. Basis for designation: outgroup comparison and character correlation.

Character 15. Elytral disc, microsculpture, mesh pattern. Three states: plesiotypic, isodiametric; apotypic, transverse; and apotypic, isodiametric, 15^{R-}, reversal. Basis for designation: outgroup comparison and group trends in Carabidae, for postulation of the plesiotypic condition; character correlation for postulation of the reversals.

Character 16. Elytral intervals, form. Three states: plesiotypic, all intervals convex; apotypic, 16^{1-}, some intervals slightly flattened; apotypic, 16^{2-}, all intervals flat. Basis for designation: outgroup comparison.

Character 17. Male fore femur, ventral brush. Two states: plesiotypic, absent; apotypic, present (Figs. 7A-D). Basis for designation: outgroup comparison.

Character 18. Female, femora, setae on ventral surface. Four states: plesiotypic, absent; apotypic, on fore femur, only, 18^{a1}; apotypic , on fore and middle femur, 18^{a2}; and apotypic, setae absent, 18^{R-}, reversal, loss. Basis for designation: outgroup comparison and character correlation.

Character 19. Frons, surface sculpture. Two states: plesiotypic, smooth; apotypic, laterally longitudinally strigose. Basis for designation: outgroup comparison.

Character 20. Elytron, number of umbilical setae. Two states: plesiotypic, 14; apotypic, 16. Basis for designation: outgroup comparison.

Character 21. Left mandible, surface of retinacular groove. Two states: plesiotypic, smooth; apotypic, strigose. Basis for designation: outgroup comparison.

Character 22. Elytron, postero-lateral angles. Two states: plesiotypic, rounded; apotypic, spinose (Figs. 15A-E). Basis for designation: outgroup comparison.

Character 23. Pronotum, position of postero-lateral setae. Two states: plesiotypic, at postero-lateral angles; apotypic, anterad postero-lateral angles. Basis for designation: outgroup comparison.

Character 24. Relative size of head and pronotum. Two states: plesiotypic, HW/PW less than 1.0; apotypic, HW/PW more than 1.0. Basis for designation: outgroup comparison.

Character 25. Elytral interneurs, punctation. Three states: plesiotypic, impunctate; apotypic, punctate; apotypic, impunctate, 25^{R-}, reversal, loss. Basis for designation: outgroup comparison, and character correlation.

Character 26. Elytron, sutural angle. Two states: plesiotypic, not spinose; apotypic, spinose. Basis for designation: outgroup comparison.

Character 27. Width of molar area of mandibles. Two states: plesiotypic, relatively narrow (Figs. 27A-B); apotypic, relatively broad. Basis for designation: outgroup comparison.

Character 28. Elytra, color. This is a complex character, and is dealt with by species group, in part. Basis for designation is in part outgroup comparison and in part character correlation. Plesiotypic, bicolored, with preapical and premedial pale fasciae against a dark background (Fig. 14A and 15A-E); apotypic, general, elytra, unicolorous dark (28*), interpreted as increase of melanin deposition.

States of elytral color are designated separately for the *transversa* group (28t), *festiva* group (28f), and the *picea* + *aerata* complex (28p). For the *transversa* group, the pattern is: plesiotypic, bicolored, with black quite extensive (Fig. 20A); apotypic, five states, showing degrees of reduction of black pigment (Figs. 20H and I, 20G, 20B and C, 20E and 20D and F; $28t^{a1-}$, $^{a2-}$, $^{a3-}$, $^{a4-}$, and $^{a5-}$).

For the *festiva* group, five states are recognized: plesiotypic, pale fasciae quite extensive (Figs. 23B-C); apotypic, with dark color decreased, and pale fasciae enlarged, joined to one another or not , two states, $28f^{a1-}$, $^{a2-}$ (Figs. 23D-E) and apotypic, pale fasciae reduced, two states, $28f^{a1}$ and ^{a2} (Figs. 23A and H).

For the *picea* + *aerata* complex, unicolorous is postulated as plesiotypic (character correlation), with various reversals to the bicolored condition: apotypic, basal half of elytron pale, $28p^{a-}$ (Fig. 33E); apotypic, large pale preapical spot $28p^{b-}$ (Fig. 33D); and apotypic, large part of disc pale, lateral margins dark $28p^{c-}$ (Figs. 33A-C). Basis for designation: character correlation.

Character 29. Middle tibia of male, preapical notch. Two states: plesiotypic, absent; apotypic, present. Basis for designation: outgroup comparison.

Character 30. Left mandible, terebral groove. Two states: plesiotypic, smooth (Fig. 2E); apotypic, strigose (Fig. 4E). Basis for designation: character correlation.

Character 31. Pronotum, posterior margin. Four states: plesiotypic, straight (Fig. 7A); apotypic, convex, 31^{a1} (Fig. 7C); apotypic, lobed, 31^{a2} (Fig. 7B); apotypic, convex, 31^{a1R-}, a reversal. Basis for designation: character correlation.

Character 32. Right mandible, terebral groove. Two states: plesiotypic, smooth; apotypic, strigose. Basis for designation: character correlation.

Character 33. Abdominal sternum VII, males. Four states: plesiotypic, posterior margin even, not notched; apotypic 33^{a1}, shallowly notched; apotypic 33^{a2}, moderately to deeply notched;

apotypic 33^{R-}, not notched, reversal. Basis for designation: outgroup comparison, and reversal postulated on the basis of character correlation.

Character 34. Right mandible, posterior retinacular area. Three states: plesiotypic, smooth; apotypic, 34^{a1}, moderately strigose; apotypic, 34^{a2}, deeply and densely strigose (Fig. 4B). Basis for designation: character correlation.

Character 35. Mandible, molar groove. Two states: plesiotypic, broadly triangular (Fig. 2E); apotypic, more linear (Figs. 3E-F, K-L). Basis for designation: character correlation.

Character 36. Mandible, terebral strigils, length and extent. Three character states: plesiotypic, short, not extended to supraterebral ridge; apotypic, 36^{1}, short, extended to supraterebral ridge (Fig. 2A); apotypic, 36^{2}, long, extended to supraterebral ridge (Fig. 4G). Basis for designation: outgroup comparison and character correlation.

Character 37. Mandible, ventral groove. Three states: plesiotypic, longer (Figs. 2C-D); apotypic, 37^{a-}, shorter (Figs. 3C-D); apotypic, absent, 37^{b-}, loss (Figs. 3I-J). Basis for designation: outgroup comparison and character correlation.

Character 38. Male abdominal sternum III, setal patch. Three states: plesiotypic, absent; apotypic, present (Fig. 10A); apotypic 38^{R-}, absent, a loss and reversal. Basis for designation: outgroup comparison and character correlation.

Character 39. Male abdominal sternum IV, setal patch. Three states: plesiotypic, absent; apotypic, 39^{a1}, present, sparse (Fig.10A); apotypic, 39^{a2}, present, dense (Fig. 10B). Basis for designation: outgroup comparison.

Character 40. Elytron, lateral margin. Two states: plesiotypic, not explanate; apotypic, explanate. Basis for designation: outgroup comparison.

Character 41. Metasternum of male, setation. Three states: plesiotypic, glabrous; apotypic, 41^{a1}, sparsely setose (Fig. 10A); apotypic, 41^{a2}, densely setose. Basis for designation: outgroup comparison.

Character 42. Head, color. Three states: plesiotypic, dark; apotypic, 42^{1-} apotypic, 42^{2-}, pale; interpreted as a loss of melanin. Basis for designation: character correlation.

Character 43. Pronotum, color. Two states: plesiotypic, dark; apotypic, 43^{-} pale, interpreted as a result of depigmentation. Basis for designation: character correlation.

Character 44. Fore tibia, upper spur. Three states: plesiotypic, normally developed (Fig. 9A); apotypic, 44^{1-}, shortened slightly (Figs. 9C-D); apotypic, 44^{2-}, reduced to a small stub (Figs. 9F-G). Basis for designation: outgroup comparison.

Character 45. Pronotum, color. Three states: plesiotypic, unicolorous; apotypic, bicolored to pale; apotypic 45^{R-} unicolorous, interpreted as a reversal. Basis for designation: outgroup comparison and character correlation.

Characters 46, 47, and 48. Male genitalia, internal sac, macrospines. The variation pattern is complex, and postulated homoplasy is substantial. For designation of character states, macrospines were postulated as ancestral for lineage C^3 (character 11^{b}). Further, three groups are postulated as ancestral (A, B, and C), and the macrospines of each spine group are postulated to have been of moderate size (*i.e.*, intermediate), with apotypic variants smaller or larger. Absence of a macrospine group is postulated to be a loss.

The basis for these postulates is as follows. All of the spine groups are present in most of the species in each of the species groups that comprise lineage M^2 (Figs. 35 and 36). Thus it seems parsimonious to infer that such would be true of the ancestral stock of lineage M^2, as well. A corollary is that absence of a spine group within lineage M^2 is the result of loss. Using moderate size as plesiotypic is based on a further postulate that ancestrally all spine groups were close to one another in size, with each group originating from similar precursors.

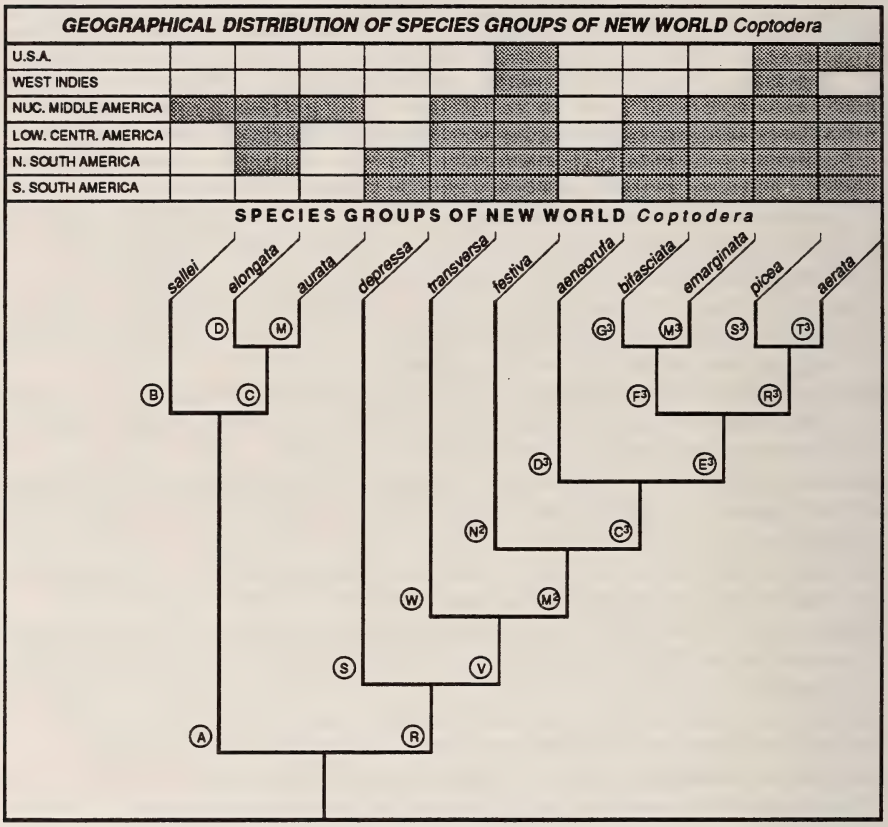


FIGURE 35. Reconstructed phylogeny of the New World species groups of the genus *Coptodera* Dejean, and their geographical distribution, in terms of major zoogeographic areas. Encircled capital letters are designations for lineages.

Character 46. Macrospine group A. Six states: plesiotypic, moderate size (Figs. 25A-B); apotypic, large, 46^{1} (Figs. 28E-F and 34A-B); apotypic, very large 46^{2} (Figs. 27A-H); apotypic, smaller, 46^{1-} (Figs. 34C-D); apotypic, very small, 46^{2-} (Figs. 34E-H); apotypic, absent, 46^{R-} (Figs. 24I-J and 28C-D), interpreted as a loss and reversal.

Character 47. Macrospine group B. Ten states: plesiotypic, size moderate, two spines (Figs. 24C-D, 27C-D, and 32A-B); apotypic, two spines, size progressively larger, 47^{1} (Figs. 24K-L), 47^{2} (Figs. 24O-P); size moderate, three spines, 47^{x} (Figs. 25A-B); apotypic, size progressively smaller, 47^{1-} (Figs. 28C-D), 47^{2-} (Figs. 34E-F), and 47^{3-} (Figs. 34G-H); apotypic, size moderate, one spine, 47^{R1-} (Figs. 24G-H and 27A-B); and macrospine group B absent, 47^{R2-} (Figs. 24A-B) interpreted as a reversal and loss. The basis for postulating two

as plesiotypic for macrospine group B is that this is the more common than, and at least as widespread as, the other numbers combined.

Character 48. Macrospine group C. Seven states: plesiotypic, size moderate, two spines (Figs. 27C-F; apotypic, size progressively larger, 48^{1} (Figs. 24A-B), and 48^{2} (Figs. 29I-J, 29K-L); apotypic, size progressively smaller, two spines, $48^{1\text{-}}$ (Figs. 27A-B), and $48^{2\text{-}}$ (Figs. 34E-F); size moderate, one spine, $48^{R1\text{-}}$ (Figs. 25A-B); and macrospine group C absent, $48^{R2\text{-}}$ (Figs. 32A-B). See explanation under macrospine group C above, for designation of spine number.

Character 49. Median lobe, form of ventral surface. Two states: plesiotypic, curved; apotypic, straight (Figs. 24C, E, M and O). Basis for designation: character correlation.

Character 50. Tarsal claws, pectination, size of pectens. Three states: plesiotypic, size moderate, extended over much of ventral surface of claw (Fig. 9E); apotypic, pectens enlarged (Fig. 8H); apotypic, $48^{\text{-}}$, pectens reduced, restricted to basal area of each claw (Fig. 9B). Basis for designation: the state postulated as plesiotypic is the most widespread, being represented in all species groups of *Coptodera*. The same result would be obtained by character correlation or functional outgroup-ingroup comparison.

Character 51. Mandible, relative length of terebra. Three states: plesiotypic, elongate (Figs. 2A-B, 3A-B, and 3G-H); apotypic, $51^{1\text{-}}$, reduced moderately (Figs. 4G-H); apotypic, $51^{2\text{-}}$, reduced markedly (Figs. 4A-B). Basis for designation: character correlation.

Character 52. Male, mid tarsus, adhesive vestiture. Two states: plesiotypic, absent; apotypic, present. Basis for designation: outgroup comparison.

Character 53. Elytron, apical margin near suture. Two states: plesiotypic, straight; apotypic, sinuate. Basis for designation: outgroup comparison.

Character 54. Clypeus and frons, surface. Two states: plesiotypic, glabrous; apotypic, setose. Basis for designation: character correlation.

Character 55. Antennomeres 5-11, sensory pits. Two states: plesiotypic, absent; apotypic, present. Basis for designation: outgroup comparison and character correlation.

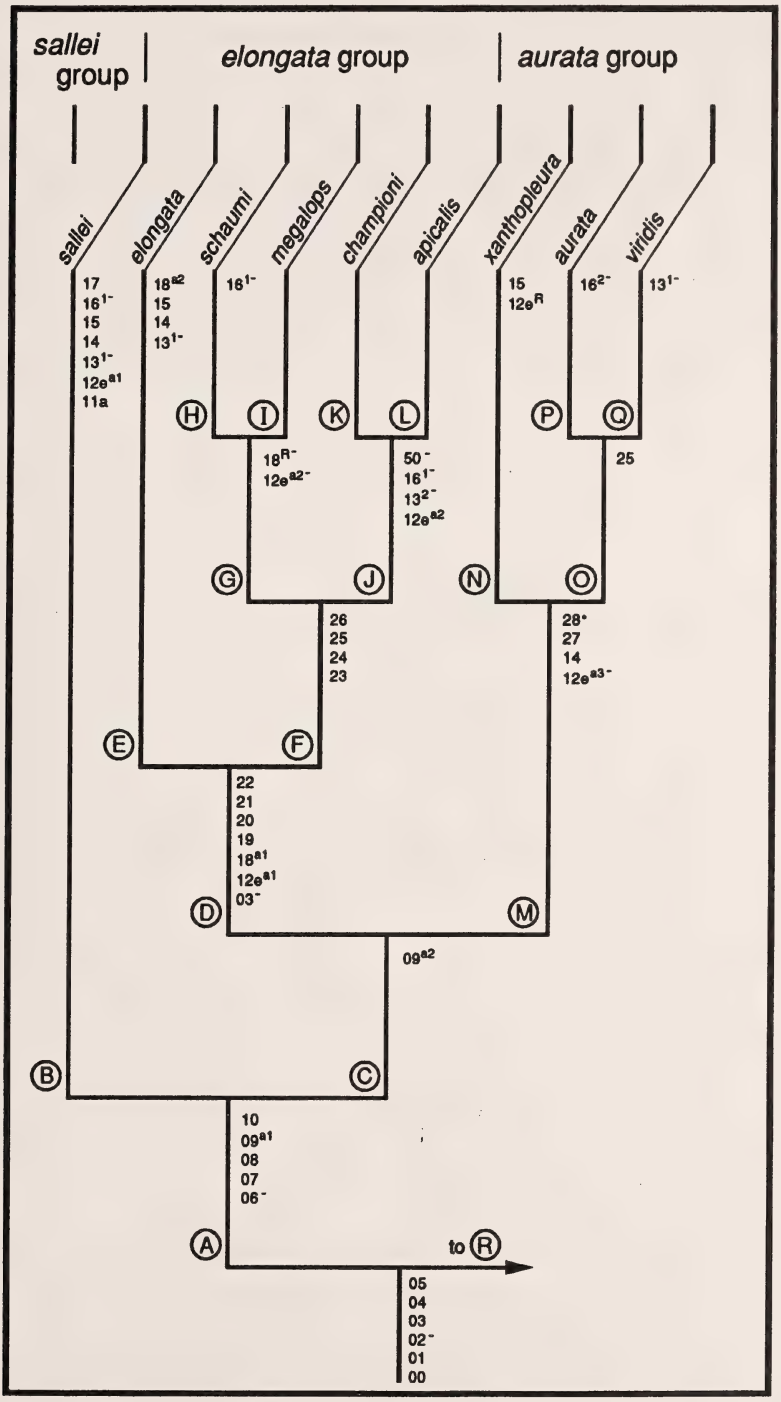
Character 56. Vertex of head, surface. Two states: plesiotypic, glabrous; apotypic, setose. Basis for designation: outgroup comparison and character correlation.

Evolution of structural features

An evolutionary analysis of a taxon seeks correlations of holomorphological patterns with habitat occupied and with way of life. Such correlation permits postulation of the details of the holomorphological features as adaptations to the environment, or the partial fitting of species to the "habitat template" (Southwood 1987). For *Coptodera*, although the general pattern of way of life has been identified (see above), the details are not known that would permit access to the holistic and highly enlightening "habitat template approach" of adaptational analysis (Spence 1989: 2445-2446). Instead, attention is drawn to the cladistic patterns postulated (*cf.* Figs. 35 and 36), with the expectation that such focus will facilitate discovery of the information needed for a more integrated and informative synthesis. Following is a series of comments, based on the reconstructed phylogeny presented in Fig. 36, intended to focus attention on the characters and their states as parts of adaptive complexes rather than as symbols for manipulation in a cladistic context.

General features.-- Table XIII shows that of 136 character states presented in the phylogenetic analysis, approximately one third arose more than once—from two to nine times. Some of these convergences are postulated reversals. Character states evolving the most frequently (nine times

FIGURE 36. Reconstructed phylogeny of the New World species of the genus *Coptodera* Dejean: *C. sallei*, *C. elongata* and *C. aurata* groups. Encircled capital letters are designations for lineages. Numbers and associated lower-case letters designate apotypic character states. See Table XII and text for details.


sallei group
elongata group
aurata group
sallei
elongata
schaumi
megalops
championi
apicalis
xanthopleura
aurata
viridis
17
16[1-]
15
14
13[1-]
12e[a1]
11a
18[a2]
15
14
13[1-]
16[1-]
16[2-]
13[1-]
15
12e[R]
H
I
K
L
P
Q
18[R-]
12e[a2-]
50[-]
16[1-]
13[2-]
12e[a2]
25
G
J
N
O
26
25
24
23
28*
27
14
12e[a3-]
E
F
22
21
20
19
18[a1]
12e[a1]
03[-]
D
M
09[a2]
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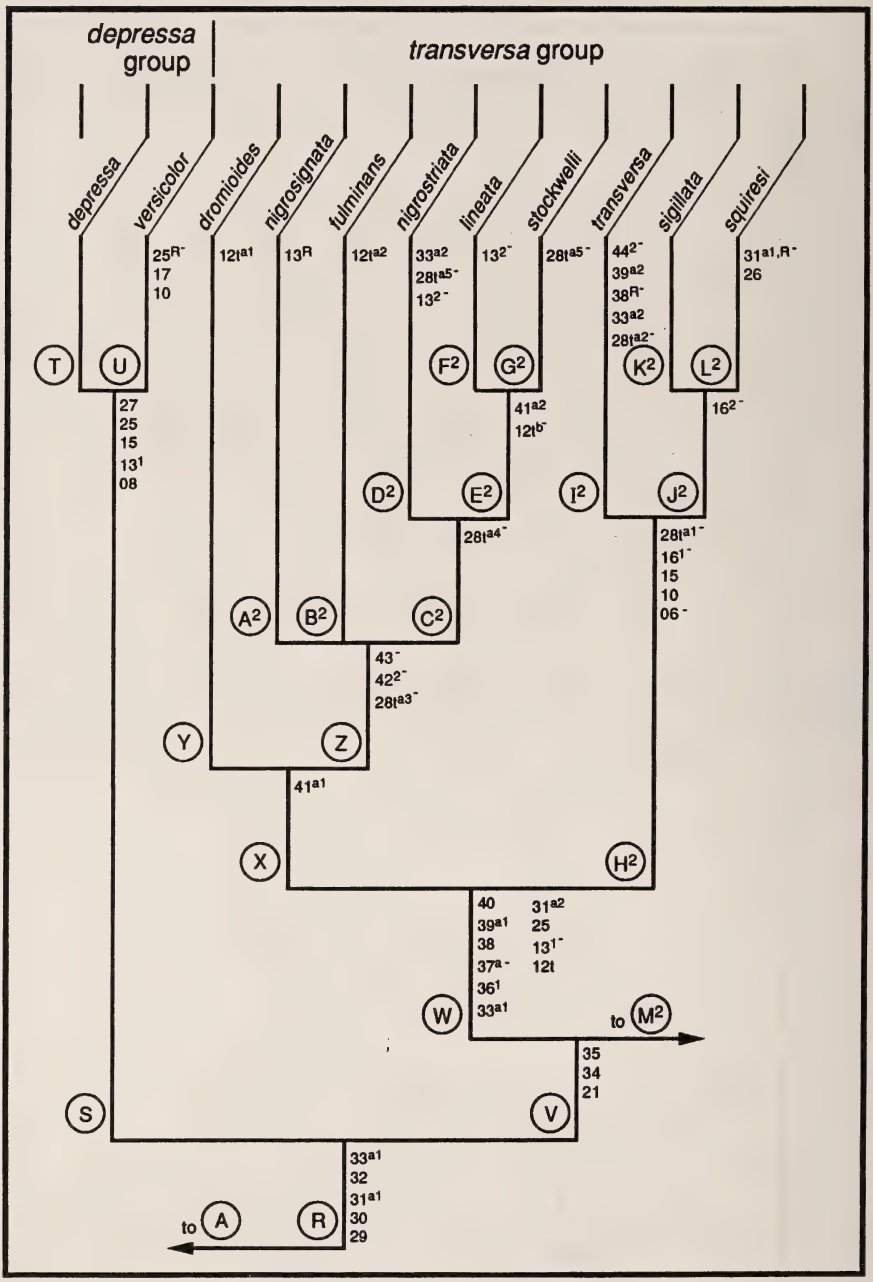


FIGURE 36 - continued. *Coptodera depressa* and *C. transversa* groups.

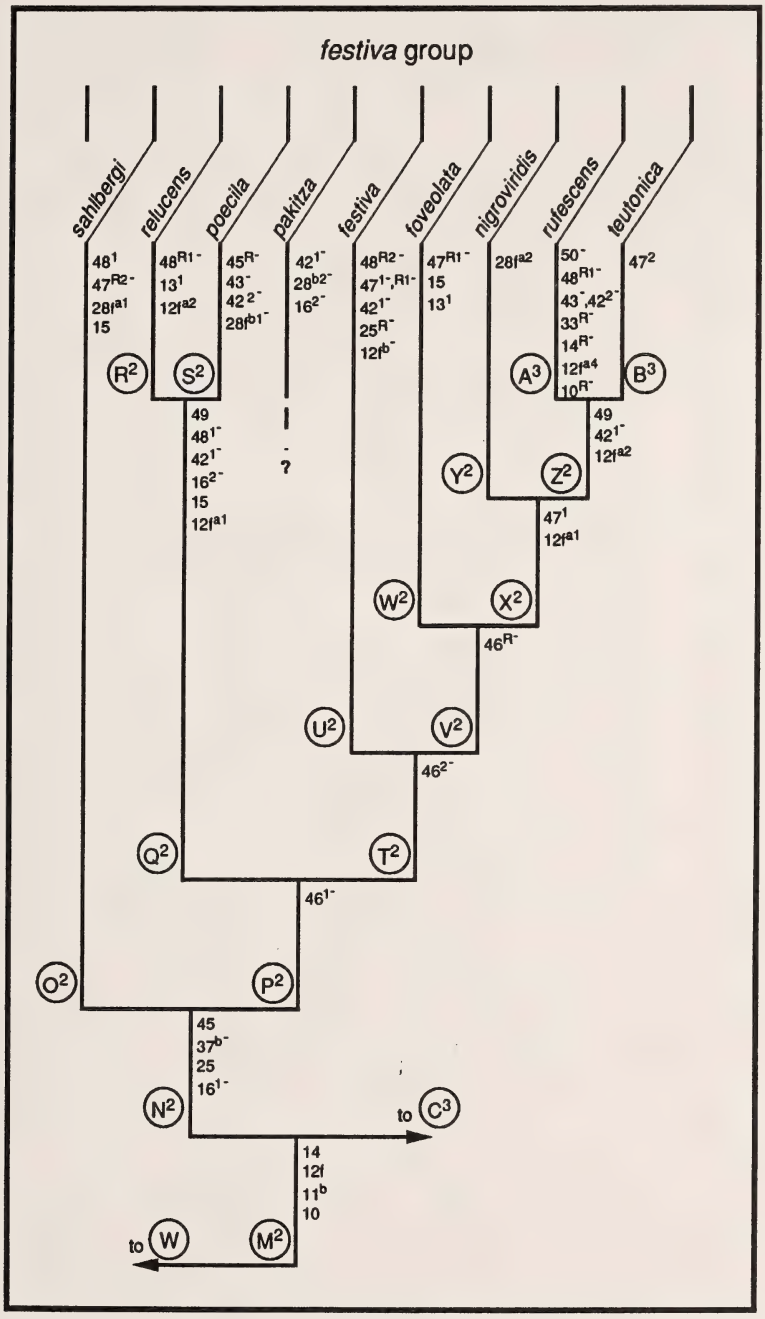


FIGURE 36 - continued. *Coptodera festiva* group.

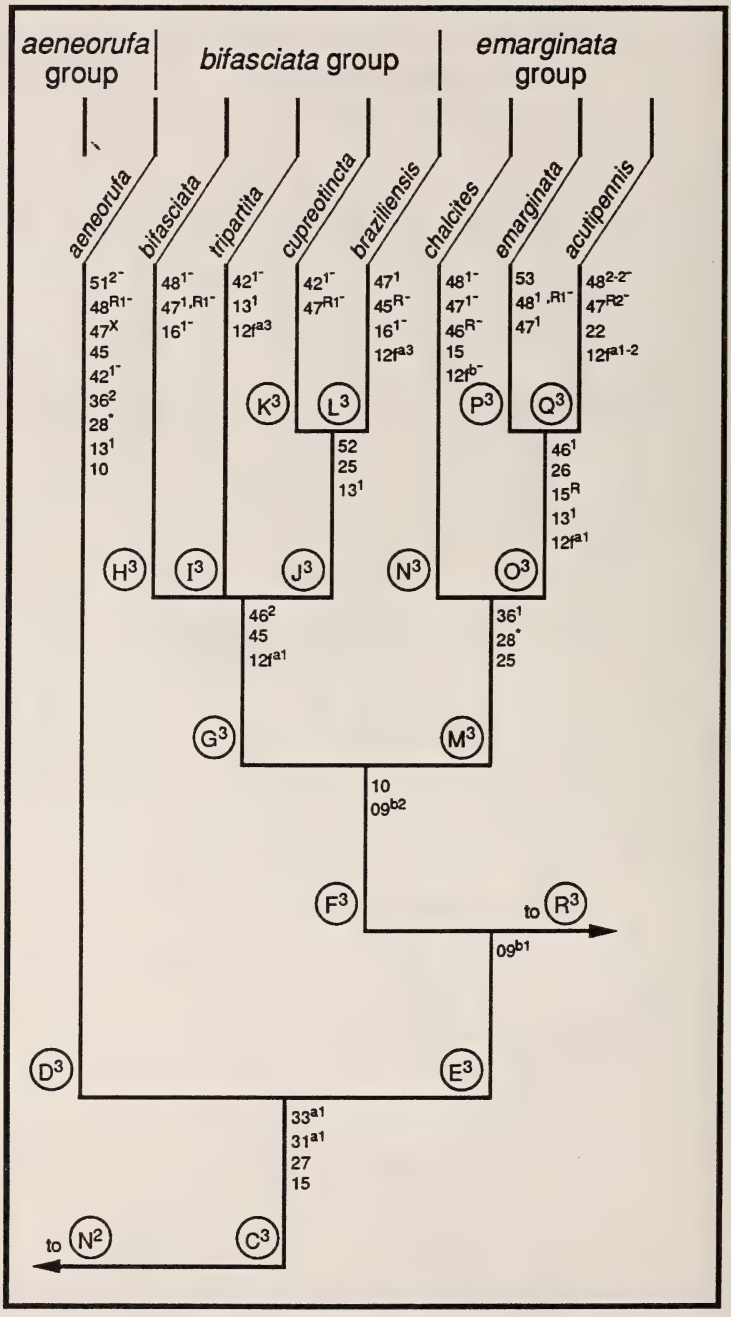


FIGURE 36 - continued. *Coptodera aeneorufa*, *C. bifasciata* and *C. emarginata* groups.

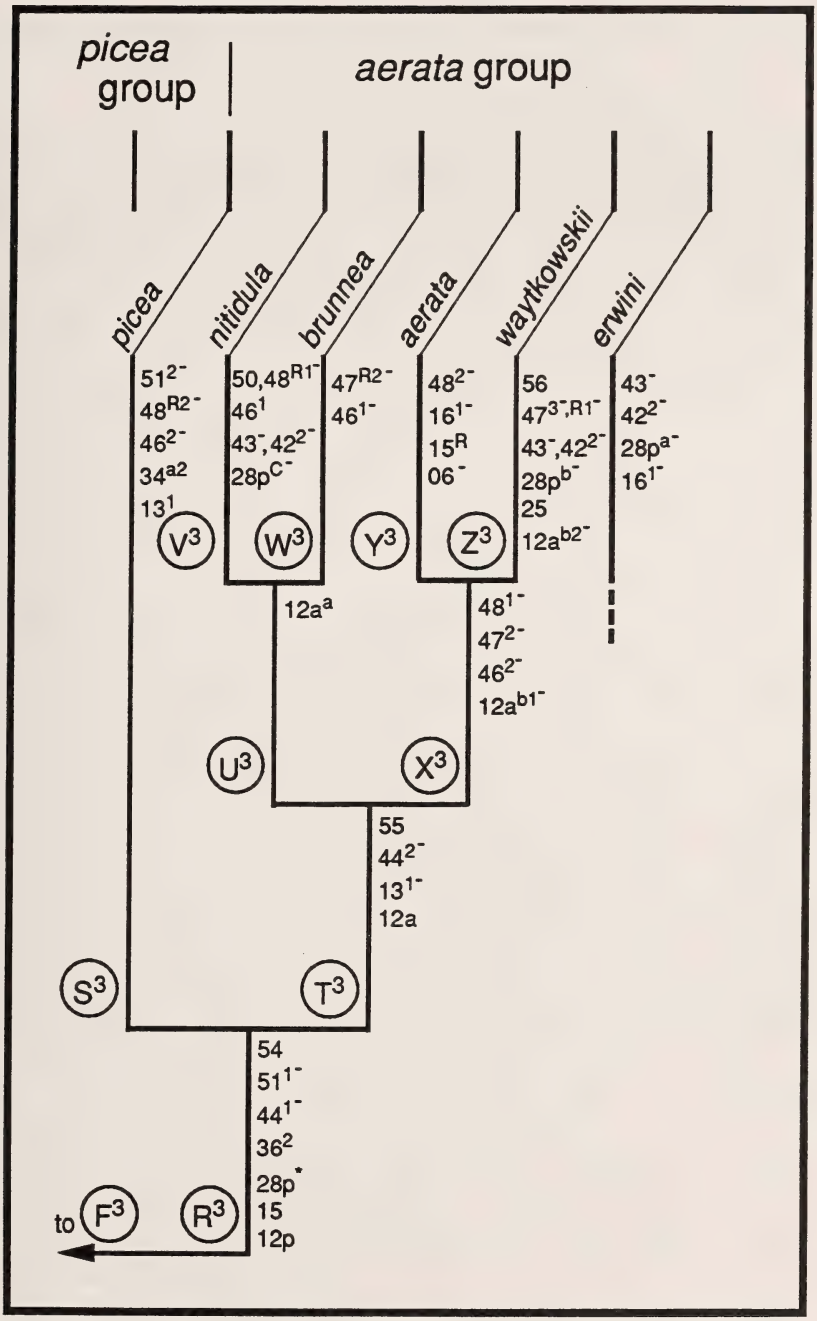


FIGURE 36 - continued. *Coptodera picea* and *C. aerata* groups.

TABLE XII. Characters and distributions of phylogenetically designated character states among the New World species of the genus *Coptodera* Dejean. See text for explanation of details.

	CHARACTERS AND CHARACTER STATES														
SPECIES	**00**	**01**	**02**	**03**	**04**	**05**	**06**	**07**	**08**	**09**	**10**	**11**	**12**	**13**	**14**
sallei	x	x	x^{-}	x	x	x	x^{-}	x	x	x^{a1}	x	x^{a}	$x_e{}^{a1}$	x^{1-}	x
elongata	x	x	x^{-}	x^{-}	x	x	x^{-}	x	x	x^{a2}	x	—	$x_e{}^{a1}$	x^{1-}	x
schaumi	x	x	x^{-}	x^{-}	x	x	x^{-}	x	x	x^{a2}	x	—	$x_e{}^{a2-}$	—	—
megalops	x	x	x^{-}	x^{-}	x	x	x^{-}	x	x	x^{a2}	x	—	$x_e{}^{a2-}$	—	—
championi	x	x	x^{-}	x^{-}	x	x	x^{-}	x	x	x^{a2}	x	—	$x_e{}^{a2}$	x^{2-}	—
apicalis	x	x	x^{-}	x^{-}	x	x	x^{-}	x	x	x^{a2}	x	—	$x_e{}^{a2}$	x^{2-}	—
xanthopleura	x	x	x^{-}	x	x	x	x^{-}	x	x	x^{a2}	x	—	$x_e{}^{a3-R}$	—	x
aurata	x	x	x^{-}	x	x	x	x^{-}	x	x	x^{a2}	x	—	$x_e{}^{a3-}$	—	x
viridis	x	x	x^{-}	x	x	x	x^{-}	x	x	x^{a2}	x	—	$x_e{}^{a3-}$	x^{1-}	x
depressa	x	x	x^{-}	x	x	x	—	—	x	—	—	—	—	x^{1}	—
versicolor	x	x	x^{-}	x	x	x	—	—	x	—	x	—	—	x^{1}	—
dromioides	x	x	x^{-}	x	x	x	—	—	—	—	—	—	$x_t{}^{a1}$	x^{1-}	—
nigrosignata	x	x	x^{-}	x	x	x	—	—	—	—	—	—	x_t	x^{R}	—
fulminans	x	x	x^{-}	x	x	x	—	—	—	—	—	—	$x_t{}^{a2}$	x^{1-}	—
nigrostriata	x	x	x^{-}	x	x	x	—	—	—	—	—	—	x_t	x^{2-}	—
lineata	x	x	x^{-}	x	x	x	—	—	—	—	—	—	$x_t{}^{b-}$	x^{2-}	—
stockwelli	x	x	x^{-}	x	x	x	—	—	—	—	—	—	$x_t{}^{b-}$	x^{1-}	—
transversa	x	x	x^{-}	x	x	x	x^{-}	—	—	—	x	—	x_t	x^{1-}	—
sigillata	x	x	x^{-}	x	x	x	x^{-}	—	—	—	x	—	x_t	x^{1-}	—
squiresi	x	x	x^{-}	x	x	x	x^{-}	—	—	?	x	?	?	?	—
sahlbergi	x	x	x^{-}	x	x	x	—	—	—	—	x	x^{b}	x_t	—	x
relucens	x	x	x^{-}	x	x	x	—	—	—	—	x	x^{b}	$x_t{}^{a2}$	x^{1}	x
poecila	x	x	x^{-}	x	x	x	—	—	—	—	x	x^{b}	$x_t{}^{a1}$	—	x
pakitza	x	x	x^{-}	x	x	x	—	—	—	?	x	?	?	?	x
festiva	x	x	x^{-}	x	x	x	—	—	—	—	x	x^{b}	$x_t{}^{b-}$	—	x
foveolata	x	x	x^{-}	x	x	x	—	—	—	—	x	x^{b}	x_t	x^{1}	x
nigroviridis	x	x	x^{-}	x	x	x	—	—	—	—	x	x^{b}	$x_t{}^{a1}$	—	x
rufescens	x	x	x^{-}	x	x	x	—	—	—	—	x^{R-}	x^{b}	$x_t{}^{a4}$	—	x^{R-}
teutonica	x	x	x^{-}	x	x	x	—	—	—	—	x	x^{b}	$x_t{}^{a2}$	—	x
aeneorufa	x	x	x^{-}	x	x	x	—	—	—	—	x	x^{b}	—	x^{1}	x
bifasciata	x	x	x^{-}	x	x	x	—	—	—	x^{b2}	x	x^{b}	$x_t{}^{a1}$	—	x
tripartita	x	x	x^{-}	x	x	x	—	—	—	x^{b2}	x	x^{b}	$x_t{}^{a3}$	x^{1-}	x
cupreolincta	x	x	x^{-}	x	x	x	—	—	—	x^{b2}	x	x^{b}	$x_t{}^{a1}$	x^{1}	x
braziliensis	x	x	x^{-}	x	x	x	—	—	—	x^{b2}	x	x^{b}	$x_t{}^{a3}$	x^{1}	x
chalcites	x	x	x^{-}	x	x	x	—	—	—	x^{b2}	x	x^{b}	$x_t{}^{b-}$	—	x
emarginata	x	x		x	x	x	—	—	—	x^{b2}	x	x^{b}	$x_t{}^{a1}$	x^{1}	x
acutipennis	x	x	x^{-}	x	x	x	—	—	—	x^{b2}	x	x^{b}	$x_t{}^{a1}$	x^{1}	x
picea	x	x	x^{-}	x	x	x	—	—	—	x^{b1}	x	x^{b}	x_p	x^{1}	x
nitidula	x	x	x^{-}	x	x	x	—	—	—	x^{b1}	x	x^{b}	$x_a{}^{a}$	x^{1-}	x
brunnea	x	x	x^{-}	x	x	x	—	—	—	x^{b1}	x	x^{b}	$x_a{}^{a}$	x^{1-}	x
aerata	x	x	x^{-}	x	x	x	x^{-}	—	—	x^{b1}	x	x^{b}	$x_a{}^{b1-}$	x^{1-}	x
waytkowskii	x	x	x^{-}	x	x	x	—	—	—	x^{b1}	x	x^{b}	$x_a{}^{b2-}$	x^{1-}	x
erwini	x	x	x^{-}	x	x	x	—	—	—	?	x	?	?	?	x

LEGEND : — plesiotypic, x apotypic, ? absent data

TABLE XII - continued - 2.

	CHARACTERS AND CHARACTER STATES													
SPECIES	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**
sallei	x	x^{1-}	x	—	—	—	—	—	—	—	—	—	—	—
elongata	x	—	—	x^{a2}	x	x	x	x	—	—	—	—	—	—
schaumi	—	x^{1-}	—	x^{R-}	x	x	x	x	x	x	x	x	—	—
megalops	—	—	—	x^{R-}	x	x	x	x	x	x	x	x	—	—
championi	—	x^{1-}	—	x^{a1}	x	x	x	x	x	x	x	x	—	—
apicalis	—	x^{1-}	—	x^{a1}	x	x	x	x	x	x	x	x	—	—
xanthopleura	x	—	—	—	—	—	—	—	—	—	—	—	x	x*
aurata	—	x^{2-}	—	—	—	—	—	—	—	—	x	—	x	x*
viridis	—	—	—	—	—	—	—	—	—	—	x	—	x	x*
depressa	x	—	—	—	—	—	—	—	—	—	x	—	x	—
versicolor	x	—	x	—	—	—	—	—	—	—	x^{R-}	—	x	—
dromioides	—	—	—	—	—	—	x	—	—	—	x	—	—	—
nigrosignata	—	—	—	—	—	—	x	—	—	—	x	—	—	x_t^{a3-}
fulminans	—	—	—	—	—	—	x	—	—	—	x	—	—	x_t^{a3-}
nigrostriata	—	—	—	—	—	—	x	—	—	—	x	—	—	x_t^{a5-}
lineata	—	—	—	—	—	—	x	—	—	—	x	—	—	x_t^{a4-}
stockwelli	—	—	—	—	—	—	x	—	—	—	x	—	—	x_t^{a5-}
transversa	x	x^{1-}	—	—	—	—	x	—	—	—	x	—	—	x_t^{a2-}
sigillata	x	x^{2-}	—	—	—	—	x	—	—	—	x	—	—	x_t^{a1-}
squiresi	x	x^{2-}	—	—	—	—	x	—	—	—	x	x	—	x_t^{a1-}
sahlbergi	x	x^{1-}	—	—	—	—	x	—	—	—	x	—	—	x_f^{a1}
relucens	x	x^{2-}	—	—	—	—	x	—	—	—	x	—	—	—
poecila	x	x^{2-}	—	—	—	—	x	—	—	—	x	—	—	x_f^{b1-}
pakitza	—	x^{2-}	—	—	—	—	x	—	—	—	x	—	—	x_f^{b2-}
festiva	—	x^{1-}	—	—	—	—	x	—	—	—	x^{R-}	—	—	—
foveolata	x	x^{1-}	—	—	—	—	x	—	—	—	x	—	—	—
nigroviridis	—	x^{1-}	—	—	—	—	x	—	—	—	x	—	—	x_f^{a2}
rufescens	—	x^{1-}	—	—	—	—	x	—	—	—	x	—	—	—
teutonica	—	x^{1-}	—	—	—	—	x	—	—	—	x	—	—	—
aeneorufa	x	—	—	—	—	—	x	—	—	—	—	—	x	x*
bifasciata	x	x^{1-}	—	—	—	—	x	—	—	—	—	—	x	—
tripartita	x	—	—	—	—	—	x	—	—	—	—	—	x	—
cupreotincta	x	—	—	—	—	—	x	—	—	—	x	—	x	—
braziliensis	x	x^{1-}	—	—	—	—	x	—	—	—	x	—	x	—
chalcites	x	—	—	—	—	—	x	—	—	—	x	—	x	x*
emarginata	x^{R}	—	—	—	—	—	x	—	—	—	x	x	x	x*
acutipennis	x^{R}	—	—	—	—	—	x	—	—	—	x	x	x	x*
picea	x	—	—	—	—	—	x	—	—	—	—	—	x	x_p*
nitidula	x	—	—	—	—	—	x	—	—	—	—	—	x	x_p^{c-}
brunnea	x	—	—	—	—	—	x	—	—	—	—	—	x	x_p
aerata	x^{R}	x^{1-}	—	—	—	—	x	—	—	—	—	—	x	x_p
waytkowskii	x	—	—	—	—	—	x	—	—	—	x	—	x	x_p^{b}
erwini	x	x^{1-}	—	—	—	—	x	—	—	—	—	—	x	x_p^{a-}

LEGEND : — plesiotypic, x apotypic, ? absent data

TABLE XII - continued - 3.

	CHARACTERS AND CHARACTER STATES													
SPECIES	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**
sallei	—	—	—	—	—	—	—	—	—	—	—	—	—	—
elongata	—	—	—	—	—	—	—	—	—	—	—	—	—	—
schaumi	—	—	—	—	—	—	—	—	—	—	—	—	—	—
megalops	—	—	—	—	—	—	—	—	—	—	—	—	—	—
championi	—	—	—	—	—	—	—	—	—	—	—	—	—	—
apicalis	—	—	—	—	—	—	—	—	—	—	—	—	—	—
xanthopleura	—	—	—	—	—	—	—	—	—	—	—	—	—	—
aurata	—	—	—	—	—	—	—	—	—	—	—	—	—	—
viridis	—	—	—	—	—	—	—	—	—	—	—	—	—	—
depressa	x	x	x^{a1}	x	x^{a1}	—	—	—	—	—	—	—	—	—
versicolor	x	x	x^{a1}	x	x^{a1}	—	—	—	—	—	—	—	—	—
dromioides	x	x	x^{a2}	x	x^{a1}	x^{a1}	x	x^{1}	x^{a-}	x	x^{a1}	x	x^{a1}	—
nigrosignata	x	x	x^{a2}	x	x^{a1}	x^{a1}	x	x^{1}	x^{a-}	x	x^{a1}	x	x^{a1}	x^{2-}
fulminans	x	x	x^{a2}	x	x^{a1}	x^{a1}	x	x^{1}	x^{a-}	x	x^{a1}	x	x^{a1}	x^{2-}
nigrostriata	x	x	x^{a2}	x	x^{a2}	x^{a1}	x	x^{1}	x^{a-}	x	x^{a1}	x	x^{a1}	x^{2-}
lineata	x	x	x^{a2}	x	x^{a1}	x^{a1}	x	x^{1}	x^{a-}	x	x^{a1}	x	x^{a2}	x^{2-}
stockwelli	x	x	x^{a2}	x	x^{a1}	x^{a1}	x	x^{1}	x^{a-}	x	x^{a1}	x	x^{a2}	x^{2-}
transversa	x	x	x^{a2}	x	x^{a1}	x^{a1}	x	x^{1}	x^{a-}	x^{R-}	x^{a2}	x	—	—
sigillata	x	x	x^{a2}	x	x^{a1}	x^{a1}	x	x^{1}	x^{a-}	x	x^{a1}	x	—	—
squiresi	x	x	x^{a1R-}	x	?	x^{a1}	x	x^{1}	x^{a-}	?	?	x	—	—
sahlbergi	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	—	x^{b-}	—	—	—	—	—
relucens	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	—	x^{b-}	—	—	—	—	x^{1-}
poecila	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	—	x^{b-}	—	—	—	—	x^{2-}
pakitza	x	x	x^{a1}	x	?	x^{a1}	x	—	x^{b-}	?	?	—	—	x^{1-}
festiva	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	—	x^{b-}	—	—	—	—	x^{1-}
foveolata	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	—	x^{b-}	—	—	—	—	—
nigroviridis	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	—	x^{b-}	—	—	—	—	—
rufescens	x	x	x^{a1}	x	x^{R-}	x^{a1}	x	—	x^{b-}	—	—	—	—	x^{2-}
teutonica	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	—	x^{b-}	—	—	—	—	x^{1-}
aeneorufa	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	x^{2}	—	—	—	—	—	x^{1-}
bifasciata	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	—	—	—	—	—	—	—
tripartita	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	—	—	—	—	—	—	x^{1-}
cupreotincta	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	—	—	—	—	—	—	x^{1-}
braziliensis	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	—	—	—	—	—	—	—
chalcites	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	x^{1}	—	—	—	—	—	—
emarginata	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	x^{1}	—	—	—	—	—	—
acutipennis	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	x^{1}	—	—	—	—	—	—
picea	x	x	x^{a1}	x	x^{a1}	x^{a2}	x	x^{2}	—	—	—	—	—	—
nitidula	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	x^{2}	—	—	—	—	—	x^{2-}
brunnea	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	x^{2}	—	—	—	—	—	—
aerata	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	x^{2}	—	—	—	—	—	—
waytkowskii	x	x	x^{a1}	x	x^{a1}	x^{a1}	x	x^{2}	—	—	—	—	—	x^{2-}
erwini	x	x	x^{a1}	x	?	x^{a1}	x	x^{2}	—	?	?	—	—	x^{2-}

LEGEND : — plesiotypic, x apotypic, ? absent data

TABLE XII - continued - 4.

	CHARACTERS AND CHARACTER STATES													
SPECIES	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**
sallei	—	—	—	—	—	—	—	—	—	—	—	—	—	—
elongata	—	—	—	—	—	—	—	—	—	—	—	—	—	—
schaumi	—	—	—	—	—	—	—	—	—	—	—	—	—	—
megalops	—	—	—	—	—	—	—	—	—	—	—	—	—	—
championi	—	—	—	—	—	—	—	x^{-}	—	—	—	—	—	—
apicalis	—	—	—	—	—	—	—	x^{-}	—	—	—	—	—	—
xanthopleura	—	—	—	—	—	—	—	—	—	—	—	—	—	—
aurata	—	—	—	—	—	—	—	—	—	—	—	—	—	—
viridis	—	—	—	—	—	—	—	—	—	—	—	—	—	—
depressa	—	—	—	—	—	—	—	—	—	—	—	—	—	—
versicolor	—	—	—	—	—	—	—	—	—	—	—	—	—	—
dromioides	—	—	—	—	—	—	—	—	—	—	—	—	—	—
nigrosignata	x^{-}	—	—	—	—	—	—	—	—	—	—	—	—	—
fulminans	x^{-}	—	—	—	—	—	—	—	—	—	—	—	—	—
nigrostriata	x^{-}	—	—	—	—	—	—	—	—	—	—	—	—	—
lineata	x^{-}	—	—	—	—	—	—	—	—	—	—	—	—	—
stockwelli	x^{-}	—	—	—	—	—	—	—	—	—	—	—	—	—
transversa	—	x^{2-}	—	—	—	—	—	—	—	—	—	—	—	—
sigillata	—	—	—	—	—	—	—	—	—	—	—	—	—	—
squiresi	—	—	—	?	?	?	?	—	—	—	—	—	—	—
sahlbergi	—	—	x	—	x^{R2-}	x^{1}	—	—	—	—	—	—	—	—
relucens	—	—	x	x^{1-}	—	x^{R1-}	x	—	—	—	—	—	—	—
poecila	x^{-}	—	x^{R-}	x^{1-}	—	x^{1-}	x	—	—	—	—	—	—	—
pakitza	—	—	x	?	?	?	?	—	—	—	—	—	—	—
festiva	—	—	x	x^{2-}	$x^{1;R1-}$	x^{R2-}	—	—	—	—	—	—	—	—
foveolata	—	—	x	x^{R-}	x^{R1-}	—	—	—	—	—	—	—	—	—
nigroviridis	—	—	x	x^{R-}	x^{1}	—	—	—	—	—	—	—	—	—
rufescens	x^{-}	—	x	x^{R-}	x^{1}	x^{R1-}	x	x^{-}	—	—	—	—	—	—
teutonica	—	—	x	x^{R-}	x^{2}	—	x	—	—	—	—	—	—	—
aeneorufa	—	—	x	—	x^{x}	x^{R1-}	—	—	x^{2-}	—	—	—	—	—
bifasciata	—	—	x	x^{2}	$x^{1,R1-}$	x^{1-}	—	—	—	—	—	—	—	—
tripartita	—	—	x	x^{2}	—	—	—	—	—	—	—	—	—	—
cupreotincta	—	—	x	x^{2}	x^{R1-}	—	—	—	—	x	—	—	—	—
braziliensis	—	—	x	x^{2}	x^{1}	—	—	—	—	x	—	—	—	—
chalcites	—	—	—	x^{R-}	x^{1-}	x^{1-}	—	—	—	—	—	—	—	—
emarginata	—	—	—	x^{1}	x^{1}	$x^{1;R1-}$	—	—	x^{2-}	—	x	—	—	—
acutipennis	—	—	—	x^{1-b2-}	x^{R2-}	x^{2-2-}	—	—	—	—	—	—	—	—
picea	—	x^{1-}	—	x^{2-}	—	x^{R2-}	—	—	x^{2-}	—	—	x	—	—
nitidula	x^{-}	x^{2-}	—	x^{1}	—	x^{R1-}	—	x	x^{1-}	—	—	x	x	—
brunnea	—	x^{2-}	—	x^{1-}	x^{R2-}	—	—	—	x^{1-}	—	—	x	x	—
aerata	—	x^{2-}	—	x^{2-}	x^{2-}	x^{2-}	—	—	x^{1-}	—	—	x	x	—
waytkowskii	x^{-}	x^{2-}	—	x^{2-}	x^{3-}	x^{1-}	—	—	x^{1-}	—	—	x	x	x
erwini	x^{-}	x^{2-}	—	?	?	?	?	—	x^{1-}	—	—	x	x	—

LEGEND : — plesiotypic, x apotypic, ? absent data

TABLE XIII. Frequency of appearance of apotypic character states among the New World species of *Coptodera* Dejean.

No. of Character States	No. of Independent Appearances
84	1
22	2
13	3
4	4
2	5
7	6
1	7
1	8
2	9
Total 136	

each) are transverse microsculpture of the elytra (character 15) and slight flattening of the elytral intervals (character 16^{1-}). Punctation of elytral intervals (character 25) evolved eight times.

Character 13, which evolved seven times, involves the membranous portion of the median lobe. The significance of such a change is not evident.

Character reversals.-- Apparent plesiotypic states are postulated to have arisen from apotypic states a total of 27 times, in 14 characters. For overall appearance, a dull dorsal surface has evolved from a shiny surface once (*C. xanthopleura*); isodiametric microsculpture of the elytra has evolved from the transverse patterns twice (in *C. emarginata* and *C. aerata*). Reversals in color pattern have occurred: for the pronotum, unicolorous has evolved from bicolored (*C. poecila*); and for the elytra, bicolored has evolved from unicolorous three times (in *C. nitidula*, *C. waytkowskii*, and *C. erwini*). The basal lobe of the pronotum has been reduced once (in *C. squiresi*).

For setation, a patch of setae on the ventral surface of the fore femora of females, a postulated synapotypy of the *elongata* group (lineage D), is postulated to have been lost once in lineage G (*C. schaumi* and *C. megalops*).

Fourteen reversals and reductions in number of parts have occurred in the macrospine complement of the male genitalia: macrospine A has been lost twice (once in lineage V^2, the *C. foveolata-nigroviridis-rufescens-teutonica* lineage; and once in *C. chalcites*); macrospine group B has been reduced to a single spine four times (*C. festiva*, *foveolata*, *bifasciata*, and *cupreotincta*), and lost once (in *C. sahlbergi*); macrospine group C has been reduced to a single spine five times (in *C. relucens*, *foveolata*, *aeneorufa*, *emarginata*, and *nitidula*), and lost twice (in *C. festiva* and *C. picea*).

These rather numerous reversals suggest that the genetic bases of these structural features are rather simple, and that direction of selection is not sustained.

Body size.-- This feature was not used in reconstructing the phylogeny of *Coptodera*. Nonetheless, size is an important characteristic of evolution of taxa, and so it is included as an aspect of the evolutionary analysis. Figure 37 illustrates for species groups the range of body size in mm., and mid-point of the range, in terms of Standardized Body Length. Most species groups, including the less derived lineages (descendants of lineage A, Fig. 35), and the basal *depressa* group of the more derived lineage R, are represented in the range 5.5-7.5 mm. Accordingly, we accept this range as ancestral.

Evolution of body size, then, has been in two directions: reduction and increase. Size has decreased in the *transversa* group (lineage W) and in lineage R^3, including the *picea* and *aerata* species groups. These two assemblages are not closely related, and so body size must have been reduced twice. Also, larger size has evolved independently three times: in the *C. elongata, festiva,* and *emarginata* groups.

No overall phyletic pattern in size variation is evident. Liebherr (1988: 158) summarizes the biological significance of increased and decreased body size. The significance of such changes in *Coptodera* are not known.

Body form.-- Explanation of the elytra (character 40) evolved in the *transversa* group (lineage W). This change is correlated with a more variegated color pattern and overall paler color.

A different change in body form involves relative head size (character 24), which evolved in lineage F, of the *elongata* group. The members of this lineage resemble members of the genus *Pericalus* Macleay, the adelphotaxon of *Coptodera*. Probably this change has to do with improved vision posteriorly, or vision all around.

Explanation of the pronotum evolved in four lineages (B, E, M, and M^2), with a reversal in *C. rufescens*, a member of lineage M^2. This change seems not to be correlated with other changes in body form.

Appearance of the dorsal surface.-- The following comments focus on the elytra because these sclerites comprise most of the dorsal surface, and exhibit for this area most of the features that were used in the phylogenetic analysis. A dull surface (character 10) is postulated to be plesiotypic for the New World species of *Coptodera*, even though this state is confined to adults of the *C. depressa* (lineage S) and *transversa* (lineage X) species groups. A shining or lustrous surface is correlated with metallic color and less precisely with transverse microsculpture (character 15). Also correlated with a lustrous surface is smoothness, meaning for *Coptodera* adults with more or less flattened elytral intervals (character 16).

Ball and Shpeley (1983: 800) suggest that the glint from a lustrous surface can "confuse a predator about the exact position of its prey, thus giving the latter an enhanced probability of escape". Erwin (1979b: 547-548) notes that a lustrous surface ("metallic coloration") is correlated with individuals that are surface-active in searching for food and mates. As recorded above, most species of *Coptodera* seem to be surface-active, on tree trunks and branches, or on the ground, at night, including species of the *transversa* group that exhibit a dull surface. Thus, a simple ecological correlate with lustrousness is elusive. Nonetheless, if our postulate is correct that a lustrous surface is derived, then strong selection is favoring development and maintenance of such a condition, an inference based on the numerous times postulated for its development and the generally parallel development of transverse microsculpture.

Punctation of the elytral interneurs (character 25) must influence appearance of the dorsal surface also, but we do not know what the influence might be. We note that, because of its frequent derivation in *Coptodera*, selection for punctate interneurs must be marked.

Color pattern of the dorsal surface.-- Color was analyzed as four characters: head (dark or pale, character 42); pronotum (dark or pale, character 43; and unicolorous or bicolored, character 45); and elytra (dark, bicolored with pale fasciae; and pale, bicolored with dark fasciae, character 28). The postulated ancestral pattern is: head and pronotum uniformly dark, and elytra bicolored—two pale fasciae on a dark background.

Fig. 38 is a diagram representing our concept of evolution of color pattern. Organized hierarchically, three groups of derived patterns are recognized: 1, dorsal surface unicolorous (1A; subsequently, depigmentation occurred, as noted below); 2, elytra bicolored, with dark fasciae against a pale background (2A and 2B); and 3, pronotum bicolored, and elytra bicolored with

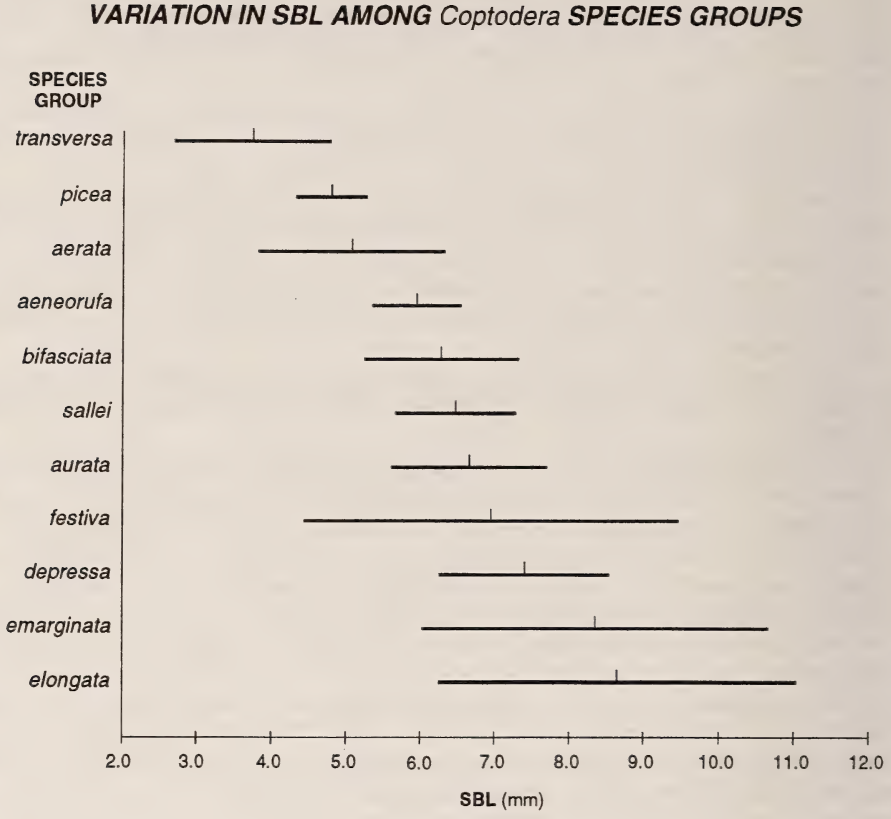


FIGURE 37. Range of variation in Standardized Body Length (in mm) among the New World species groups of the genus *Coptodera* Dejean.

background dark and fasciae pale (Figs. 3A and 3B). Each of these basic types was modified further, as noted below.

Of 26 possible derived patterns (excluding reversals), only seven are known: (1), dark head, pronotum, and elytra (frontispiece, and Fig. 38, 1A; evolved in three groups, independently—*aurata* [lineage M], *emarginata* [lineage M^3], and the *picea-aerata* lineage [R^3]); (2), dark head, dark pronotum, and bicolored elytra (Figs. 20B-F) with pale background and dark fasciae (Fig. 38, 2A; evolved in the *transversa* group once [lineage H^2]); (3), dark head, bicolored pronotum, and bicolored elytra, with dark background (Fig. 38, 3A-3B; evolved twice—once in the *festiva* group [sahlbergi—lineage O^2], and once in the *bifasciata* group [lineage G^3]); (4), bicolored head, bicolored pronotum, and bicolored elytra with background dark (Fig. 38, 3B; evolved five times

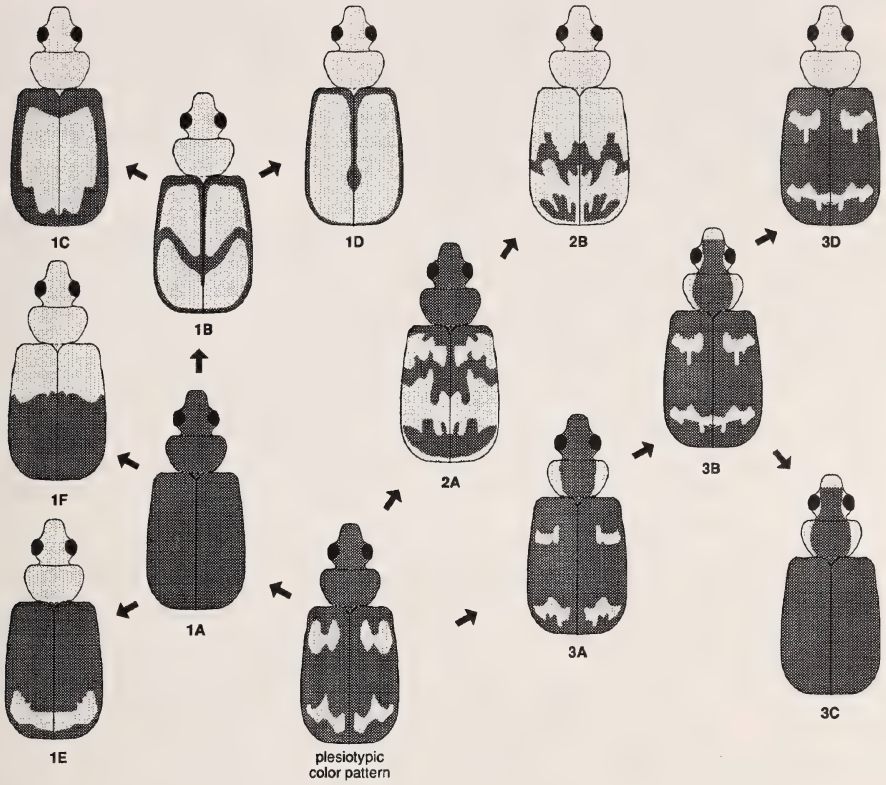


FIGURE 38. Diagram of postulated evolution of color pattern of the dorsal surface among species of the genus *Coptodera* Dejean in the New World.

—three times in the *festiva* group [*relucens*--lineage R^2, *festiva*--lineage U^2, and *teutonica*--lineage B^3], and twice in the *bifasciata* group [*tripartita*--lineage I^3, and *cupreotincta*--lineage K^3]; (5), bicolored head, bicolored pronotum, and dark elytra (Fig. 38, 3C; evolved once, in *aeneorufa* [lineage D^3]); (6), head pale, pronotum pale, and elytra bicolored with dark background (Fig. 3D; evolved four times, twice in the *festiva* group [*C. poecila*--lineage S^2, and *rufescens*--lineage A^3], and twice in the *aerata* group [*nitidula*--lineage V^3, and *waytkowskii*--lineage Z^3]; and (7), head pale, pronotum pale, and elytra bicolored with background pale and fasciae dark (Fig. 2B; evolved once, in the *transversa* group [lineage Z]).

In the *C. aerata* group, partial depigmentation has produced bicolored elytra three times (*C. nitidula* [Fig. 38, 1B-1D; Figs. 33A-C], *waytkowskii* [Fig. 38, 1E; 33D], and *erwini* [Fig. 38, 1F; 33E]). Although the character state "bicolored" is regarded as plesiotypic for the elytra of *Coptodera*, its appearance in the *C. aerata* group is a derived condition, and represents a reversal.

Note, however, that the pattern is not the same as in those taxa with plesiotypically bicolored elytra.

Short, parallel trends in reduction of dark color are represented by the adelphotaxa *C. relucens-poecila* and *C. teutonica-rufescens*: the first member of each species pair has the head and pronotum bicolored, whereas in the second member, these sclerites are completely pale. In general, a trend in reduction of dark pigment is evident in the *C. transversa, festiva, aeneorufa* and *bifasciata* groups. In the *C. transversa* group, pigment reduction of the head and pronotum seems to have been a single step (dark to pale). In the others, a two-step process is evident: from dark to bicolored, and from bicolored to completely pale.

Erwin (1979b: 547) suggests that color and color pattern of arboreal carabids are the result of selection caused by predators. The relatively few combinations that have been realized and the development more than once of some combinations suggest that color pattern is important in the adaptation to their habitats of the species of *Coptodera*.

Sense organs.-- Ventral pits on the flagellar articles that house sensory setae evolved once in lineage T^3 (*C. aerata* group, Figs. 1A-B). Such structures have evolved also in several other groups of lebiines (subtribe Metallicina, and Celaenephina). Other evolution of sense organs involves number, size and position of tactile setae (characters 01, 03, 06, 07, 20, and 23). The long setae on the palpigers (character 01) characteristic of the pericaloid assemblage, must enhance the sensory component of the mouthparts, but the advantages of the other changes affecting sensory organs is not apparent.

Mouthparts.-- Apotypic features of the mouthparts are recorded as 11 characters: 02 (edentate mentum, Figs. 6A-D); 08 (notched anterior margin of labrum, Figs. 1C-H); and 21, 27, 30, 32, 34, 36, 37, and 51 (various aspects of the mandibles, Figs. 2A-H, 3A-L, and 4A-L). Changes in details of mandibular structure include: surface grooving (characters 21, 30, 32, 34 and 36); shortening of the terebra or lengthening of the basal area (character 51); widening of the molar area (character 27); narrowing of the molar groove (character 35); and loss of the ventral groove (character 37). Loss of the ventral grooves was preceded by loss of the ventral microtrichia which probably are involved in transfer to the mouth of liquified bits of prey (Evans and Forsythe 1985: 115). Such loss suggests that the mandibles of *Coptodera* adults are used only for prey capture, or that only particulate matter is transferred to the mouth *i.e.*, that digestion is solely post-oral, and not pre-oral. The system of parallel strigils or grooves on various parts of the occlusal margins might be indicative of improved holding or shredding surfaces. Increase in size of the molar area might have to do with an enhanced crushing ability, crushing being the normal function of this region.

Overall, there is a marked transformation in the mandibles, associated with the reconstructed phylogeny. Among the more primitive lineages (A and its descendants), *C. sallei* exhibits no apotypic features (Figs. 2A-F), and the *aurata* and *elongata* groups exhibit one apotypy each. Of the more basal stocks of the more derived lineages (R and its descendants), the *C. depressa* group (S and its descendants) exhibits two mandibular apotypies, whereas for the remaining taxa (V and its descendants) the number of apotypies ranges from five (*bifasciata* group) to eight (*emarginata, picea* [Figs. 4A-F], and *aerata* [Figs. 4G-L] groups). This trend suggests some changes in feeding methods, and possibly in food consumed.

Elytra.-- Surface luster and sculpture of the elytra are discussed above. Here, we note development of spines posteriorly (characters 22 and 26). The postero-lateral angles have become spinose in the *elongata* group (lineage D, Fig. 15A), only. The sutural angles have become spinose three times, once each in the *elongata* (lineage F, Figs. 15B-E), *transversa* (lineage L^2, Fig. 20I) and *emarginata* (lineage O^3,Figs. Figs. 28A-B) groups.

As Erwin (1979b: 552-553) notes, spinose elytra of New World Lebiini are almost confined to tropical arboreal species. He suggests that such spines might have evolved as "antipredation" devices, perhaps functioning to prevent being swallowed by predators.

Legs.-- Excluding setation (see above, under evolution of secondary sexual features), only two features of the legs show variation. The upper spur of the fore tibia (character 44) has been reduced in one lineage (R^3, Figs. 9C-D), and then lost (lineage T^3, Figs. 9F-G). This spine has been lost also from lineage I^2 (*C. transversa*). Pectens of the tarsal claws (character 50) have become markedly reduced in lineage J (*C. championi-apicalis*, Fig. 9B) and in lineage A^3 (*C. rufescens*).

The significance of these changes is not immediately apparent. The upper tibial spur is part of the antenna cleaning organ. Its loss (known to have occurred in other lebiine groups, such as *Lebia* and *Euproctinus*) may indicate a change in function of the cleaning organ. The reduced pectination of the tarsal claws may represent a change in detailed mechanism of gripping the substrate. Perhaps with fewer points of contact of claws with substrate, a beetle is able to move more rapidly, though it might have to avoid smoother surfaces.

Stylomere 2 of the ovipositor.-- Normally, the ensiform setae are located on the dorsal margin of stylomere 2. In the *C. sallei* and *elongata* groups (lineages B and D, respectively), however, probably independently, these setae have shifted to a more lateral position (character 07, Figs. 11A-D). The functional significance of this shift is not apparent.

Secondary sexual characters.-- Six secondary sexual features (characters 17, 29, 33, 38, 39 and 52) are exhibited by males, and one (character 8) is exhibited by females, involving primarily patches of setae, variously distributed. Most of these apotypic states are confined to single groups: 18 (setae on the femora), to the *C. elongata* group (lineage D); 38 and 39 (setal patches on abdominal sterna and metasternum Figs. 9A-B, to the *transversa* group (lineage W); and 52 (adhesive vestiture on tarsomeres of middle legs) to the *bifasciata* group (lineage J^3). Character 17 (setal patches on the ventral surfaces of the fore femora) occurs only in *C. sallei* (Figs. 7A-B) and *C. versicolor* (Figs. 7C-D), each occurrence being an independent development.The apotypic state of character 29 (notched middle tibia of males) and 33 (notched abdominal sternum VII) characterize lineage R and its descendants—the largest assemblage of New World *Coptodera*. Mid-tibial notches are known also in the genus *Lebia* (Madge 1967: 147). Possibly they are used by males as an additional device to hold on to females, gripping the edges of the elytra during mating.

Thus, secondary sexual characters range in distribution from a few to many species. The setal patches could be involved in release of pheromones, while the adhesive devices may provide enhanced ability of males to hold on to females during mating.

Male genitalia.-- The males of each New World species of *Coptodera* exhibit distinctive genitalia, differing variously from their putatively close relatives in form and proportions of the median lobe, position of the ostium, and in size and number of macrospines of the internal sac. Eight characters (numbers 09, 11, 12, 13, 46, 47, 48 and 49) and 54 character states of the genitalia were recognized. Such tendency for interspecific differentiation suggests that, at times in the history of lineages, the genitalia were labile, a suggestion borne out in the remarkable variation exhibited by males of *C. acutipennis*, in which nine morphs are distinguishable.

Position of the ostium (character 09) exhibits distinctive trends, from nearly catopic in the more primitive lineages (descendants of lineage A, Figs. 14B-C, and 16A-J) to anopic (Figs. 34A-H) and pleuropic-right (Figs. 27A-H, and 28C-F) in the most derived lineages (descendants of lineage E^3). Fig. 39 is a diagram, illustrating the hypothesized evolution of this character.

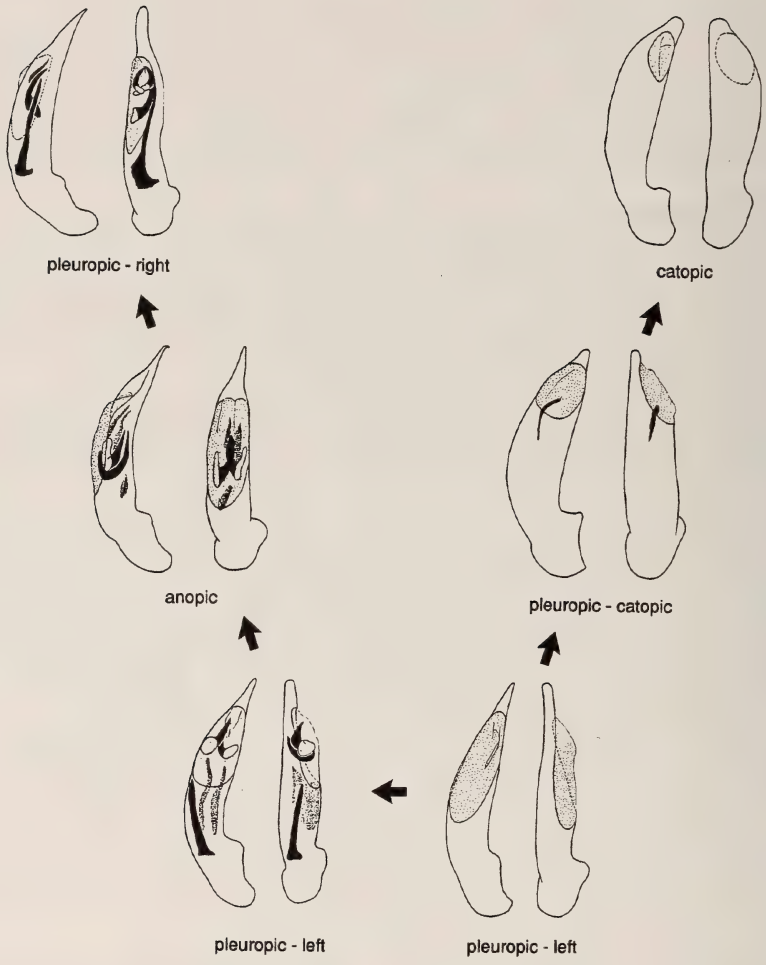


FIGURE 39. Diagram of postulated evolution of the median lobe of the male genitalia among species of the genus *Coptodera* Dejean in the New World.

The more derived lineages (descendants of lineage M^2) are characterized by having macrospines on the internal sac (characters 46-48; cf. Figs. 24A-N). Otherwise, the pattern of genitalic variation seems almost random.

Summary of character evolution.-- The evolutionary pattern overall is simple in that most sequences of change are short, each such involving development of an apotypic state followed by stasis or reversal, and without continued specialization of the apotypy. The evolutionary pattern is complex, however, in terms of convergences and reversals, as indicated in Table XIII and Fig. 36, and as discussed above. Such a pattern may be a reflection of the seemingly slight ecological differentiation of the genus, with lineages being subjected repeatedly to the same kinds of selective forces, but in different combinations in different geographical areas, and under oscillating climatic regimes. The only marked shift in way of life seems to be that of departure from close association with tree trunks and loosened bark to life in the leaf litter and association with fruitfalls. A consistent feature of *C. acutipennis*, and a varying feature of *C. festiva* and *C. cupreotincta*, this ecological change is not accompanied by any striking structural changes.

Why, then, are there so many species of *Coptodera* in the New World? Perhaps this diversity has to do with features related to reproduction rather than those associated with day to day maintenance. Certainly, secondary sexual features characterize the major South American stock of *Coptodera* (lineage R), and the most varied character system is that of the male genitalia; the latter system may be involved with development of reproductive isolation. Thus, geographical isolates may tend to differentiate in such features. That geographical isolation has occurred frequently in the history of *Coptodera* is indicated by distribution patterns of extant taxa, as discussed below.

Geographical history of the New World species of *Coptodera*

Introduction.-- Maps 1-20 illustrate the known geographical ranges of the species of *Coptodera*, and are basic empirical components of this analysis. The theoretical component is the general theory of evolution of distribution patterns of Neotropical taxa that have been developed during the past half century by biogeographers and geologists. For general background information see, in particular, publications by Hershkovitz (1966 and 1972), Whitehead (1976), Schreiber (1978), Noonan (1979), Erwin (1979a), Savage (1982), Stehli and Webb (1985a), and Halffter (1987). For zoogeographical analyses of taxa of Carabidae with ranges comparable to those of *Coptodera*, see references in Noonan (1985), and the discussion below, under "Comparisons".

The distribution pattern of *Coptodera* in the New World is presented in terms of species diversity and postulated interspecific relationships. A general synthesis is based on correlating the chorological patterns and the reconstructed phylogeny of the New World species of *Coptodera*.

TABLE XIV. Diversity of New World species of *Coptodera* Dejean by 10° intervals of latitude.

Latitude	No. Species
40-50 N.	1
30-40 N.	3
20-30 N.	11
10-20 N.	15
0-10 N.	21
0-10 S.	23
10-20 S.	22
20-30 S.	16
30-40 S.	1

The distribution pattern: species diversity.-- Latitudinally, species number is maximal equatorially and decreases north and south, as summarized in Table XIV. Of the 43 known species of *Coptodera*, the ranges of 29 are confined to the tropics. The ranges of 14 species extend beyond the tropics: two (*C. brunnea* and *aerata*), north of the Tropic of Cancer, only; 10, south of the Tropic of Capricorn, only; and two (*C. picea* and *nitidula*), both north of the Tropic of Cancer and south of the Tropic of Capricorn. The range of only one species (*C. aerata*) is completely outside of the tropics (to the north).

The geographical distribution of *Coptodera* was analyzed as well in terms of biogeographical zones or areas (or morphoclimatic domains [Heyer 1988: 265]) that have more or less distinctive assemblages of species of this genus or that have been recognized on the basis of distribution patterns of other taxa (see, for example, Willink 1988: 207, Fig. 1). Each zone, designated by a capital letter, and its approximate geographical limits is indicated in Table XV and on Map 21. Table XVI illustrates species ranges in terms of these zones.

The zones with the largest number of species are: C (Amazon Basin); A (Southern Atlantic Forest and environs); and H (Nuclear Central America). Together, zones A and C have 29 species, or about two-thirds of the New World *Coptodera* fauna.

The species of *Coptodera* occupy from one to 10 zones (Tables XVI and XVII). Nearly half (20) of the species are known from single zones (Table XVII), and of these, 14 are in zones A (Southern Atlantic Forest and environs) and C (Amazon Basin). The remaining single zone precinctives are distributed among five zones. Six zones are without precinctives.

While interpreting these numbers, it is important to consider that seven of these single-zone precinctive species are known from few specimens and each from a single locality (zone A--*C. sigillata*, *squiresi*, and *teutonica*; zone C--*C. pakitza* and *erwini*; zone G--*C. poecila*; and zone J--*C. foveolata*). Almost certainly, the ranges of these species are more extensive, and may extend into other zones. However, it is unlikely that additional information about the ranges of these species will alter the overall patterns appreciably.

At continental and sub-continental levels, Table XVI shows that 23 species are precinctive in South America, and 12 are precinctive in North America, with 10 of the latter in Middle America, only, one in the U.S.A., only, and one shared between Middle America and the southwestern United States. Eight species are shared between North and South America; of these shared species, only three enter United States, and only in the south. In summary, each continent has a distinctive set of species of *Coptodera*, with the precinctives comprising 80 percent (35/43) of the total *Coptodera* fauna.

From an evolutionary perspective, the distribution patterns, interpreted solely in terms of species diversity, indicate three major tropical centers of diversification: two in South America, with one each in the Amazon Basin and Southern Atlantic zone; and one center in tropical North America (*i.e.*, Middle America).

The distribution pattern is consistent with a major barrier between North and South America. With the West Indies having been invaded by only two species, and with *trans*-Andean South America (zone F) having only four species in contrast to the extensive *cis*-Andean assemblage, the distribution pattern is consistent with a group whose members do not cross readily open sea or extensive mountain ranges.

The distribution pattern: phylogenetic aspects.-- If differentiation of lineages has a geographical component, the latter is identified by examination of chorological affinities of related taxa. Adelphotaxa that occupy different areas point to previous connections between those areas.

TABLE XV. Zoogeographic zones for description of geographical ranges of the New World species of *Coptodera* Dejean.

Zone	
A	Southern Atlantic South America, south and east of the Amazon Basin. This corresponds approximately to the area containing the Serro do Mar and Paranese biotas (see Nores [1992: 347, Fig. 1]), or the Atlantic Forest (Vanzolini 1988: 327), and includes principally semideciduous or seasonal forest, and "rich dense forest on rolling terrain" (Brown 1982: 293, Fig. 16.33).
B	*cis*-Andean South America (Vanzolini 1988: 317), south of the Amazon Basin (*Ca.* 20°S.), between the eastern slopes of the Andes and the Southern Atlantic Zone (A). This corresponds to the dry areas between Zones A and C, and includes the Chaco, Cerrado, and Caatinga (Nores 1992: 347, Fig. 1).
C	The Amazon Basin. The general term for the forests of this great area is hylaea. In fact, the hylaea extends unbroken from the Amazon Basin to the Guianas (Vansolini 1988: 326).
D	*cis*-Andean South America, north of the Amazon Basin and west of the Northern Atlantic Zone (E).
E	*cis*-Andean South America, north of the Amazon Basin and including northern Brazil and the Guianas (the North Atlantic Zone).
F	Chocó refugium in *trans*-Andean Columbia and Ecuador (see Gentry (1982) for a discussion of the flora of this region).
G	Lower Central America, including Panamá, north to southern Nicaragua.
H	Nuclear Central America, from Northern Nicaragua to the Isthmus of Tehuantepec, in southern México.
I	México north of the Isthmus of Tehuantepec, Pacific Versant.
J	México, north of the Isthmus, Gulf (or Atlantic) Versant.
K	West Indies
L	Southwestern United States (Arizona and New Mexico)
M	Eastern United States, from Florida west to the 100th Meridian, and north to about 43°N.

TABLE XVI. Distribution of the New World species of *Coptodera* in relation to geographical zones.

DISTRIBUTION OF THE NEW WORLD SPECIES OF *Coptodera* IN RELATION TO GEOGRAPHICAL ZONES

MAP No.	SPECIES	GEOGRAPHICAL ZONES: SOUTH AMERICA A	B	C	D	E	F	MIDDLE AMERICA G	H	I	J	WEST INDIES K	U. S. A. L	M	TOTAL ZONES OCCUPIED	PRECINCTIVE IN: SOUTH AMER.	NORTH AMER.	SHARED BETWEEN S.A. & N.A.
8	*fulminans*														1			
10	*sipilata*														1			
12	*laurinesi*														1			
14	*bilasciata*														1			
14	*brazilensis*														1			
12	*rufescens*														2			
14	*thyanta*														2			
6	*deplessa*														3			
11	*sahlbergi*														1			
7	*dromioides*														4			
15	*emarginata*														4			
6	*versicolor*														1			
8	*nigrosignata*														1			
11	*relucens*														1			
11	*pakiza*														1			
15	*chalcites*														1			
20	*waytkowskii*														1			
20	*erwini*														1			
3	*megalops*														1			
9	*nigrostriata*														2			
13	*aeneorufa*														2			
4	*apicalis*														1			
10	*stockwelli*														1			
11	*porecila*														1			
2	*elongata*														3			
9	*lineata*														4			
12	*festiva*														7			
1	*sallei*														2			
5	*xanthopleura*														2			
5	*auratia*														2			
12	*nigroviridis*														2			
18	*brunnea*														3			
5	*viridis*														1			
12	*foveolata*														1			
19	*aerata*														1			
14	*cuprapotincta*														5			
10	*transversa*														8			
15	*acutipennis*														8			
16	*picea*														10			
17	*nitidula*														10			
3	*schaumi*														4			
4	*championi*														2			
	TOTAL SPECIES	17	7	21	5	8	4	12	14	6	13	2	2	3		23	13	7
	TOTAL PRECINCTIVES	6	0	8	0	0	1	2	0	1	1	0	0	1		23	13	0

TABLE XVII. Frequency distribution of number of New World species of *Coptodera* Dejean and number of zoogeographic zones occupied (see Table XVI for details).

No. Zones Occupied	No. Species
1	20
2	9
3	4
4	4
5	1
6	0
7	1
8	2
9	0
10	2
Total No. Species	43

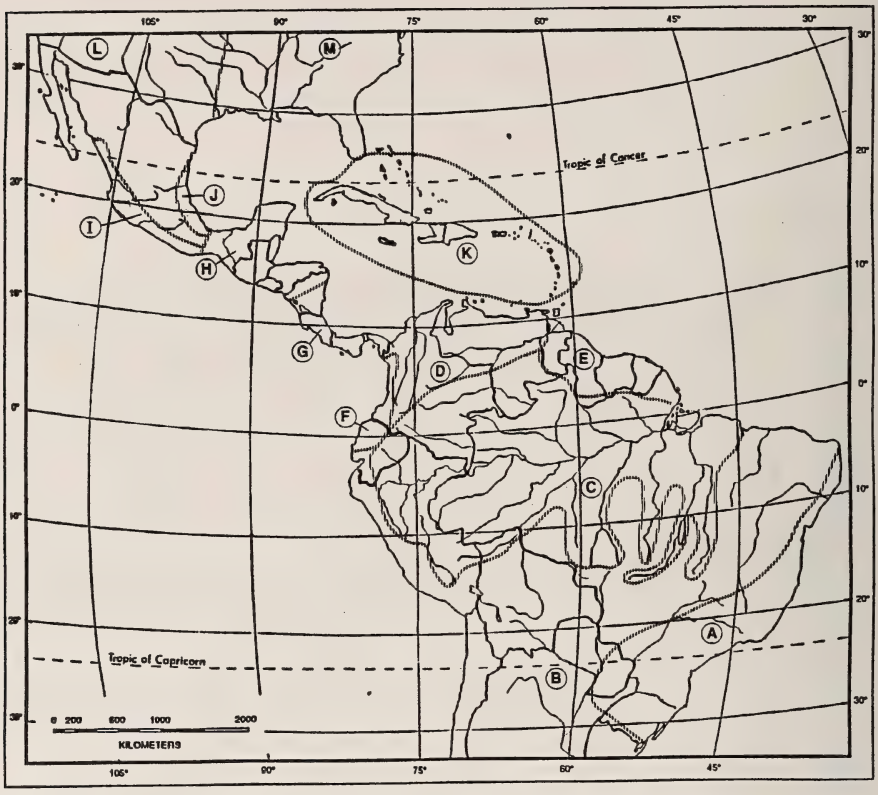
Figure 35 shows generally a broad overlap among species groups of New World *Coptodera*, indicating for most of them extensive sympatry. However, the concentration of the descendants of Lineage A in the Middle American part of North America, and conversely the concentration of descendants of lineage R in South America, is indicative of a barrier in the past between the North and South American continents.

At the level of species, in contrast, Table XVIII shows allopatric associations among eight of the 11 pairs. Putative barriers within zone A would explain the distribution of two pairs. The ranges of two pairs, though overlapping broadly or narrowly, differ sufficiently to suggest a barrier between zones A and C. A barrier between South America and Middle America would explain the chorological affinities of four pairs of allopatric species, and two pairs of species with ranges that overlap broadly or narrowly. A barrier between zones I and J would explain the chorological affinities of one species pair.

Table XIX shows the distribution pattern for second and third level groupings of taxa. For each set of adelphotaxa, each component is numbered for ease of reference. Of 14 comparisons, seven, or half, are allopatric associations, and three are narrowly sympatric. The incidence of allopatry is lower than among species pairs, but allopatry is an important component of the pattern.

Location of putative barriers among adelphotaxa is instructive: four are between zones A and C; four are between South America and Middle America; one is within zone C; one is between Lower and Nuclear Central America; and one is within zone J, on the Gulf Versant of México. As for species pairs, the putative barrier between South and Middle America is prominent for these more inclusive groups of taxa.

Summary of the evidence.-- The New World species of *Coptodera* are basically tropical, being confined to lowland and lower montane forests. Most of the species are South American, and many of the species are precinctive there. There is also a substantial Middle American fauna of *Coptodera*, with a precinctive component. The West Indies archipelago harbors only two wide-ranging species. North America north of México is marginal for the genus, with a single precinctive species in zone M.



MAP 21. Biogeographic zones for the New World species of *Coptodera* Dejean.

Although geographical ranges overlap broadly at the level of species groups, the descendants of the basal lineages (A and R) are concentrated in Middle America and South America, respectively. Within the groups allopatry and narrow sympatry are prominent features of the distribution pattern.

Based on this pattern, the following scenario is offered group by group as a reconstruction of the geographical history of *Coptodera* in the New World. The discussion is followed best by referring to the maps and to the reconstructed phylogeny (Fig. 36).

The process of development of the distribution pattern of *Coptodera* in the New World.-- Because the genus is basically Gondwanian in distribution, we postulate that the ancestral stock was part of the original South American biota, when the South American continent separated from Africa during Mesozoic time. Late in the Cretaceous period, or early in the Tertiary, an early stock of *Coptodera* reached the Middle American part of North America. South America and southern North America were either joined temporarily then, or inter-continental access was easier than it was subsequently (Fig. 40), until the development of a permanent land connection during

TABLE XVIII. Species-level adelphotaxa of the New World species of *Coptodera* Dejean and their chorological affinities.

SPECIES - LEVEL ADELPHOTAXA AND THEIR CHOROLOGICAL AFFINITIES					
MAP No.	SPECIES PAIRS	GEOGRAPHICAL ASSOCIATION			PUTATIVE BARRIERS OR AREAS OF CONTACT
		Broadly Sympatric	Narrowly Sympatric	Allopatric	
10	*sigillata - squiresi*				within zone A
12	*rufescens - teutonica*				within zone A
6	*depressa - versicolor*				between zones A & C
15	*emarginata - acutipennis*				between zones A & C
11	*relucens - poecila*				S. America / M. America
3	*schaumi - megalops*				S. America / M. America
4	*championi - apicalis*				S. America / M. America
9	*lineata - stockwelli*				S. America / M. America
17-18	*nitidula - brunnea*				S. America / M. America
19-20	*waytkowskii - aerata*				S. America / M. America
5	*aurata -viridis*				between zones I & J
	Total	2	1	8	

TABLE XIX. Two- and three-level adelphotaxa or trichotomous relationships, and their chorological affinities.

TWO - AND THREE - LEVEL ADELPHOTAXA OR TRICHOTOMOUS RELATIONSHIPS, AND THEIR CHOROLOGICAL AFFINITIES							
MAP No.	COMPONENTS OF SPECIES COMPLEXES			GEOGRAPHICAL ASSOCIATION			PUTATIVE BARRIERS OR AREAS OF CONTACT
	1	2	3	Broadly Sympatric	Narrowly Sympatric	Allopatric	
14	*bifasciata*	(*tripartita*	(*cupreo. + braz.*))	1 & 3	1 & 2 ; 2 & 3		1 / 3 - A / C ; 1 / 2 - A / C
10	*transversa*	(*sig. + squiresi*)			1 & 2		A / C
15	*chalcites*	(*emarg. + acut.*)		1 & 2			A / C
12	*nigroviridis*	(*ruf. + teutonica*)				1 & 2	M. Amer. / S. Amer.
9	*nigrostriata*	(*lin. + stockwelli*)				1 & 2	M. Amer. / S. Amer.
8-9	*nigrosignata*	(*fulminans*	(*nigst. - (lin. + stock.*))	2 & 3		1 & 2 ; 1 & 3	2 / 3 - C ; 1 / 2 - A / C ; 1 / 3 - S. Amer. / M. Amer.
12	*foveolata*	(*nigroviridis*	(*ruf. + teutonica*))			1 & 2 + 3 ; 2 & 3	1 / 2 + 3 - H / J ; 2 / 3 - M. Amer. / S. Amer.
2-4	*elongata*	((*sch. + meg.*)	(*champ. + apicalis*))	2 & 3		1 & 2 + 3	1 / 2 + 3 - S. Amer. / M. Amer.; 2 / 3 - C-D / F
			Total	4	3	7	

the Pliocene epoch (Savage 1982). Following entry into Middle America, the New World stock of *Coptodera* differentiated into a Middle American component (lineage A) and a South American component (lineage R, Fig. 35).

Coptodera sallei (lineage B, Map 1) is interpreted as a phylogenetic relict, occupying montane tropical forests on the Pacific Versant of Guatemala and on the Gulf Versant of México. The fact that this species occurs at higher altitudes only (between 1200 and 1900 m.) suggests that it has been displaced from the lowland forests that are occupied by the other species groups of *Coptodera*.

The *elongata* group (lineage D) probably differentiated first into a Nuclear American component (lineage E, Map 2), represented by *C. elongata*, and a Lower Central American-South American component, lineage F. The ranges of the descendants (lineages G and J) of the latter (Maps 3 and 4) extend into the Amazon Basin (zone C) in *cis*-Andean South America, and into the Chocó (zone F) in *trans*-Andean South America.

We postulate an initial South American differentiation for lineage F: first, a barrier oriented north-south (the Andes?) to separate descendant lineages G and J, with G to the east and J to the west. Then, we postulate a barrier oriented east-west, and that this barrier was the seaway between South America and the early Tertiary volcanic islands that comprised Lower Central America. This postulate requires a crossing of the sea barrier by both lineages G and J, with consequent differentiation of each lineage into two species. Finally, the more northern descendants, *C. schaumi* and *C. championi* that were the islandic isolates, invaded South America comparatively recently (Fig. 40). Other scenarios are possible, particularly differentiation of lineages G and J in South America, with the more northerly pair of descendants (*C. schaumi* and *C. championi*) invading Middle America comparatively recently, using the Panamanian land bridge to do so. We chose the former hypothesis because it uses a ready-made barrier—a barrier that is not so apparent on the South American continent.

Differentiation of lineage M (*aurata* group, Map 5) occurred in Middle America. The location of the barrier that produced descendant lineages N (*C. xanthopleura*) and O is not evident. Disjunction of lineage O, however, probably was associated with the orogenic events that produced the Mexican highlands in Miocene time (Kohlmann and Halffter 1990: 12), isolating ancestral *C. aurata* in the east (zone J) and ancestral *C. viridis* in the west (zone I).

Differentiation of lineage S (*depressa* group, Map 6) evidently had to do with development of a disjunction between the forests of the Amazon Basin (zone C) and those of the Southern Atlantic zone (zone A), producing in zone C ancestral *C. versicolor*, and in zone A ancestral *C. depressa*. Subsequently, *C. depressa* became more widespread, if the widely disjunct records in Colombia and Trinidad can be accepted at face value.

Differentiation of lineage X (*transversa* group, Maps 7-10) is highly complex, suggesting a sequence of disjunctions followed by differentiation and subsequent range interpenetration. Because of extensive range overlap of the various lineages and the consequent difficulty of attempting to postulate locations of range disjunctions and barriers, we confine a detailed consideration to lineages C^2 (Map 9) and H^2 (Map 10). Each of these lineages is represented in both South America and Middle America.

The species of lineage C^2 are allopatric in relation to one another, and their ranges form a line suggesting disjunctions that paralleled the reconstructed phylogeny. A disjunction between South America and Lower Central America separated lineage D^2 (ancestral *C. nigrostriata*) from lineage E^2. Subsequently, the range of the latter was divided by a barrier (probably in Lower Central America) that led to development of the extant *C. lineata*, which ranges from zone G to I and J, and *C. stockwelli*, known only from zone G, to the east of the range of *C. lineata*.

The species of lineage H^2 range over much of the same territory occupied by the species of C^2. However, all three species of H^2 are represented in the South Atlantic zone A, and it seems likely that their ranges overlap there, at least partly. A possible scenario for the differentiation of these species is the following: isolation of segments of lineage H^2 in the Amazon Basin (zone C) and the South Atlantic zone (A), the Amazonian isolate giving rise to *C. transversa*, and the South Atlantic isolate to ancestral lineage J^2. Subsequently, the range in zone A of the latter lineage was divided, the resulting isolates giving rise to the extant species *C. squiresi* and *C. sigillata*. Later, the Amazonian *C. transversa* dispersed: northward and westward, to enter and become widespread in Middle America; and southward and eastward, to enter zone A. Its apparent confinement in México to the Gulf Versant (zone J) suggests arrival there in post-Pliocene time (Halffter 1974: 227).

Lineage N^2 (*festiva* group, Maps 11 and 12) groups nine species, the combined ranges of which include all of the zoogeographic zones except L to the north, and *trans*-Andean zone F. Although *C. festiva* is on both American continents, we postulate that it is adventive in South America, being an immigrant there, or more probably, an introduction—it is known only from a locality near the mouth of the Amazon River (Map 12), and easily could have been carried there in a ship from a Caribbean port.

Lineage N^2 differentiated into O^2 (*C. sahlbergi*) and P^2, with *C. sahlbergi* centered in the South Atlantic zone (A), and probably isolated there as an early disjunct. Lineage P^2 probably occupied the Amazon Basin (zone C) and adjacent areas. The disjunctive event that led to differentiation of the latter lineage into Q^2 and T^2 probably was entrance by dispersal of the lineage into Middle America (specifically zone G, Lower Central America). The South American descendant lineage also, but subsequently, entered Lower Central America (zone G), giving rise there to lineage S^2 (ancestral *C. poecila*) and the South American vicar R^2 (in zone C), giving rise to ancestral *C. relucens*.

The Middle American lineage, T^2, differentiated sequentially to produce five extant species, two of which (*C. rufescens* and *teutonica*) are South American precinctives, in zones E and A. The localities of two of the Middle American species (*C. foveolata* and *nigroviridis*) are in zones H and J, in México, and are overlapped by the range of widespread *C. festiva* (Map 12). Probably differentiation was through disjunction, with *C. festiva* invading subsequently the ranges of its relatives.

The adelphotaxon of *C. nigroviridis* (lineage Y^2) is lineage Z^2, the ancestral stock of *C. rufescens* + *teutonica*. Evidently the common ancestor of these lineages (X^2) became widespread, dispersing southward into South America, and then eastward. With *C. rufescens* and *C. teutonica* being represented in very few localities, further comment about their differentiation is not justified.

Lineage C^3 includes the extant members of five species groups of *Coptodera* (*aeneorufa*, *bifasciata*, *emarginata*, *picea* and *aerata* groups), whose ranges are indicated on Maps 13 to 20. Most of the species are South American, and so we postulate that most of the species level evolution has taken place in South America.

The monobasic *aeneorufa* group (lineage D^3, Map 13) is widespread in the Amazon Basin, and as well enters the Guianas (zone E). Its adelphotaxon, lineage E^3, contains most of the species. The immediate descendants of lineage E^3 (F^3 and R^3) include two groups, each of which has representatives in Middle America.

The four species of lineage G^3 (*bifasciata* group, Map 14) are represented in zone A. However, *C. braziliensis* and *C. bifasciata* are known only from this zone, and their contact with the other two species, *C. tripartita* and *C. cupreotincta*, is marginal. Thus, it seems reasonable to postulate range disjunction as a means of speciation: isolation of lineage I^3 (*C. tripartita*) in the

Amazon Basin, and isolation of lineage J^3 (possibly in zone A, to the southeast), followed by dispersal and differentiation to produce ancestral *C. braziliensis* in zone A, and *C. cupreotincta* elsewhere, with the latter becoming widespread, and dispersing as far north as Nuclear Central America (zone H).

Lineage M^3 includes the three species of the *emarginata* group (Map 15). The ranges of the species pair *C. emarginata-acutipennis* (lineage O^3) are in contact marginally in zone E and probably A, with *C. acutipennis* distributed widely to the north and west, including Nuclear Middle America (zone J). The range of *C. chalcites* (lineage N^3) is in principally the Amazon Basin. We postulate a range disjunction separating N^3 and O^3, with N^3 giving rise to *C. chalcites* in the Amazon Basin, and lineage O^3 developing elsewhere, possibly in zone A. Following this differentiation, lineage O^3 became widespread, then disjunct, with the resulting isolates differentiating into the extant species *C. emarginata* and *C. acutipennis*. This latter disjunction could have occurred again between zones A and C, just as the previous disjunction that gave rise to lineages N^3 and O^3. The Amazonian range of *C. chalcites* was overlapped eventually by that of *C. acutipennis*, of lineage O^3.

Lineage R^3 includes two species groups (*picea* and *aerata*) and the most widespread species in the genus (Maps 16-20). The continent of origin of the lineage cannot be postulated directly on the basis of numbers clues: two of the descendants are precinctive species in North America; two are precinctive in South America; and two are widespread. Phylogenetically, two lineages (U^3 and W^3) have vicars on both continents. However, the distribution pattern of lineage R^3 is sufficiently similar to those of the other groups of *Coptodera* that some inferences are possible.

The monobasic *picea* group (lineage S^3, Map 16) probably originated in South America, became widespread recently, probably in post-Pliocene time, reaching the West Indies and even southern Florida, probably overwater, from Cuba (Fig. 40).

Lineage U^3 (Maps 17-20) became widespread initially, and produced two isolates: one in Nuclear Middle America (*C. brunnea*, Map 18) and one probably in South America (*C. nitidula*, Map 17). Subsequently, both taxa became more widespread, with *C. brunnea* reaching southwestern United States (zone L), and *C. nitidula* overlapping the range of *C. brunnea*, to the north. Again, the wide range of *C. nitidula* is consistent with rapid spreading northward in post-Pleistocene time (Fig. 40).

Lineage X^3 (Maps 19 and 20) followed a sequence similar initially to that of U^3, except that the two vicars (*C. aerata* precinctive in zone M, eastern United States; and *C. waytkowskii*, possibly precinctive in zone C, the Amazon Basin in tropical South America) remain separated widely. The relationships of *C. erwini* have not been determined, but probably this species is close to *C. waytkowskii*.

Summary.-- The process of diversification of *Coptodera* in the New World has been one of differentiation of geographically isolated vicars, followed by dispersal and range interpenetration of the resulting adelphotaxa. The isolation leading to differentiation has been the result of two processes: interruption of range continuity of beetle species through interruption of habitat continuity principally within South America and Middle America; and crossing of sea barriers, principally between South America and Lower Central America, by dispersing stocks. The intercontinental sea barriers probably varied in extent through time. Disruption of habitat seems to have been a recurring event, with disjunctions being repeated between adjacent zones—in particular, between zones A and C. Present intercontinental range continuity of several extant species is the result of development of a land connection between continental South America and North America (Fig. 40).

Fig. 40, which is based on the presentation above, shows 14 dispersals from South America to Middle America, and four dispersals in the opposite direction. Most of the dispersals are postulated to be relatively recent, occurring during the last few million years or so. The predominance of the south-north direction is consonant with Darlington's (1959) general theory of the direction of movement of species being from larger to smaller land areas.

Comparisons.-- In this section, to illustrate similarity in distribution, we compare the biogeographic patterns of *Coptodera* with the patterns exhibited by the following carabid taxa.

The precinctive New World pericaline eucheiloid complex (Tribe Lebiini), analyzed by Ball and Shpeley (1983: 801-803), like *Coptodera*, was postulated to have had as its principal place of evolution the South American continent. Incursions into Middle America were postulated to have occurred at various times during the Tertiary and Quaternary periods, the earlier lineages to have arrived being represented now by precinctive taxa, in Lower and Nuclear Central America, and in México north of the Isthmus of Tehuantepec. Because the species were represented by very few specimens, especially in South America, a more detailed analysis there of chorological associations and identification of possible areas of precinctivism was not possible.

With the Neotropical indigenous metallicine genus *Euproctinus* Leng and Mutchler (Tribe Lebiini), *Coptodera* shares: a Gondwanian origin (the adelphotaxon of *Euproctinus* is in the Old World Tropics [Ball and Shpeley 1986: 334]); an early differentiation, based on early entry into Middle America, and subsequent evolution there (Ball and Shpeley 1986: 339); recognition of biogeographic zones A, D, F, G, H, I, L and M, based on precinctive or indigenous taxa; postulated recent arrivals in Middle America of representatives of South American taxa; and representation in the West Indies by recent arrivals.

With the pan-tropical genus *Galerita* Fabricius (*sensu latiore*), *Coptodera* shares a vicariant splitting, isolated descendants in Old and New Worlds, and a subsequent early arrival and isolation in Middle America of a primitive stock that gave rise to subgenus *Progaleritina* Jeannel, the South American vicar becoming the subgenus *Galerita* (Ball 1985: 315). The distribution pattern of the predominantly South American and moderately diverse *americana* group has not been analyzed in sufficient detail, either phylogenetically or geographically, to make useful comparisons with other taxa, except to note Middle American taxa that suggest descendence from early arrivals, and species shared between South and Middle America suggesting recent arrival in the latter area. The Middle American subgenus *Progaleritina*, however, has been analyzed. Like *Coptodera*, *Progaleritina* has precinctive species in zones I, J, and M (Ball and Nimmo 1983: 307, Fig. 7).

With the pattern of the New World precinctive harpaline *Stenomorphus* complex of genera, *Coptodera* shares: a splitting of an early stock that gave rise in Middle America to a distinctive group (*Stenomorphus* Dejean) and in South America to its adelphotaxon (*Trichopselaphus* Chaudoir) (Ball, Shpeley and Currie 1991); indigenous components in zones G, I, and J; and later inter-continental dispersals of lineages of both genera (Ball 1978 and 1987).

The New World precinctive harpaline genus *Amblygnathus* Dejean shares with *Coptodera* evidence of an early South American/ Middle American differentiation, with the *A. iripennis* group being indigenous on the North American continent (Ball and Maddison 1987: 274). Like lineage A of *Coptodera*, the *A. iripennis* group became moderately speciose, and like the *C. aurata* species group, it produced a precinctive lineage (the *A. interior-evansi* stock) in zone I (the Pacific Versant of México). As well, there are indigenous species of *Amblygnathus* ranging within zones G and H.

The Australian-New World pterostichine genus *Loxandrus* LeConte shares with *Coptodera* a major species radiation in tropical South America, with lineages of various ages entering the North American continent, and differentiating therein. Zone I has a precinctive species, *L.*

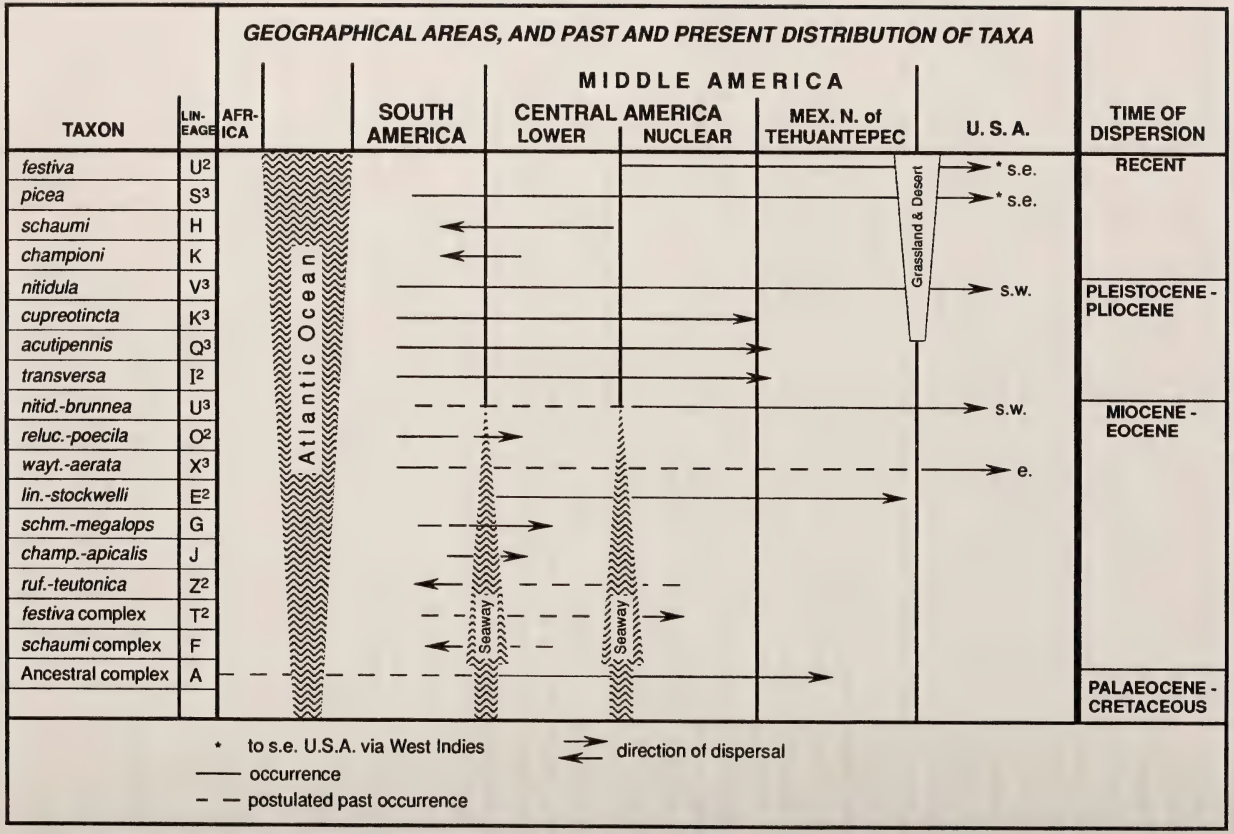


FIGURE 40. Diagram indicating postulated time and direction of intercontinental dispersals of New World species and species complexes of the genus *Coptodera* Dejean.

pactinullus Allen, and zones G, H, and J have indigenous species some of which may be single zone precinctives (Allen and Ball 1980).

In contrast to *Coptodera*, there was a major earlier Tertiary species radiation in zone M (eastern United States), whereas *Coptodera* is represented there by a single precinctive species, *C. aerata*.

Like *Coptodera*, the New World precinctive lebiine genus *Agra* Fabricius consists of arboreal species. It is markedly speciose, with an enormous South American component, but with substantial representation in Middle America, as well. Thus, *Agra* is similar to *Coptodera* in the general pattern of diversity. The genus is being studied in detail by T.L. Erwin, who has produced a series of revisions of various species groups. Only the *A. feisthameli* and *formicaria* lineages have been analyzed zoogeographically (Erwin and Pogue 1988). Both of these complexes exhibit patterns similar to those of *Coptodera*, with precinctive species in zones A, C, G + H + J, and I, referred to by Erwin and Pogue as centers of endemism. The reconstructed phylogeny indicates that descendants of the less derived lineages in Middle America have reinvaded South America, and differentiated there. This is similar to but more extensive than the biogeographical pattern of lineage T^2 of *Coptodera*.

These comparisons point to a general theme underlying evolution of taxa in the Neotropical Region. However, it is important to appreciate that each of the above-noted groups exhibits features of distribution that do not coincide with the distributional features of the other taxa. Probably each taxon responds in a distinctive manner to the forces and circumstances that determine the underlying theme—that response being determined by vagility and a unique combination of other adaptations (Noonan 1988: 366).

General paradigm of Neotropical biogeography.-- For the evolution of the tropical component of the Neotropical biota, a general explanation is emerging, based on refuge theory (Prance 1982 and references therein; Vanzolini and Heyer 1988 and references therein), and on a theory of physical and biotic connections between the North American and South American continents, including when such events took place (Stehli and Webb 1985a and references therein). These theories primarily apply to events that took place during the Cenozoic Era.

Another part of the general explanation of the evolution of the tropical component of the Neotropical biota concerns its origin. The Mesozoic-age supercontinent Gondwana is postulated to be the source area for most of the indigenous South American biota (Jeannel 1942; Noonan 1985: 336-337; Reichardt 1979).

The distribution pattern of *Coptodera* fits rather well the patterns recognized for other taxa, including temporal aspects, and strengthens thereby the general paradigm that has been developing. At the species level, many pairs of inferred adelphotaxa are distributed vicariously in lowland forest in the American tropics, suggesting surviving isolates of once more widespread lineages. Lineages inferred to be older have members that are sympatric with one another, leading to the inference that following differentiation in isolation, dispersal and range interpenetration took place. This suggests that the conditions changed (or ameliorated) that led initially to range disruption, and that the species of *Coptodera* were parts of biotic assemblages (if not integrated communities) and moved as elements of these assemblages. Such alternating sequences of dispersal and range disjunction are tenets of refuge theory, as explained and developed during the past two decades or so (Haffer 1982: 9). There are problems with the refuge theory (see Heyer 1988: 268 and Cadle and Patton 1988: 242), but it seems sound generally.

Middle America houses the principal tropical component of the North American biota. A substantial part of the Middle American biota is postulated to be South American in origin, and this postulate implies dispersal from one area to the other. Changes in intercontinental connections

have determined to some extent the timing of arrivals. In fact, the South American component of the Middle American biota consists of older and younger assemblages (Savage 1982: 473 and 477), with older elements (Savage's "Middle American Element") having arrived in Middle America in Late Cretaceous-Palaeocene time, across some form of connection that allowed easier access than was available during most of the subsequent Tertiary Period. That older component differentiated to a more or less marked extent. The present connection of the American continents was established in the late Tertiary (Stehli and Webb 1985b: 11), with the formation of a land bridge, permitting easier access than was possible with the two continents separated by a seaway. This Panamanian land bridge was used by the younger assemblage of taxa (Savage's "South American element") to enter Middle America. (According to Stehli and Webb, the Panamanian connection led to a major biotic intercontinental exchange. For a different point of view about "the Great American Interchange", and one that is more consonant with the facts of distribution of poikilothermous vertebrates and arthropods, see Hershkovitz 1966 and 1972).

As indicated above, and in conclusion, the distribution pattern of *Coptodera* fits generally this theory of a concentration in two time periods of South American lineages entering Middle America, but with the important exception that intercontinental exchange of lineages was not restricted to the periods of easier access. A number of the lineages must have entered both Middle America and South America in periods when the physical connection was interrupted by the Bolivar trench, and Lower Central America was at most a string of isolated islandic volcanos (Duellman 1979; Smith 1985: 41-43).

Concluding Remarks

When we began study of the New World species of *Coptodera*, we planned only a taxonomic treatment at the species level, intending to provide a synopsis that would be useful for identification. In the course of our work, which followed on from the analyses of two great 19th Century carabid specialists, H.W. Bates and M. de Chaudoir, both of whom published their major works on the genus in 1869, we discovered a certain amount of new synonymy, and 12 species previously unrecognized and unnamed—about 27 per cent of the total number of species recognized by us.

As information accumulated about the species, their structural features and geographical distribution, patterns began to emerge, and we were able to develop a system of hypotheses about evolutionary relationships and geographical history of *Coptodera* in the New World. We hope that these hypotheses will be useful to future workers, who will extend knowledge of this genus in holomorphological depth and in geographical breadth.

Although it is possible now to identify to species the adults of *Coptodera* from the New World and from the Afrotropical Region, the same cannot be stated about the species of the Oriental Region. Jedlička's publication (1963) is defective, but at least it provides a starting point. Habu (1967), with his fine work on the Japanese component of the *Coptodera* fauna of the eastern Palaearctic Region that is a northern extension of the Oriental fauna, has provided an excellent basis for work on the latter, and an excellent example of a taxonomic study of high quality. Darlington (1968), working on the New Guinea fauna, has clarified knowledge about the eastern end of the Oriental *Coptodera* fauna.

Once the Oriental species are known to a level of detail comparable to knowledge of the group from elsewhere, it will be possible to provide a general synthesis, which will serve to test previous work, including this study, and to provide an evolutionary treatment of a pantropical

assemblage of arboreal beetles. We would be pleased to cooperate in making such an endeavor possible.

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Appendix A

[Description of the new species *C. tripunctata* received following completion of MS]

Coptodera tripunctata, new species
Map 20

Type material.-- HOLOTYPE female, labelled: PERU: Loreto, Cocha Shinguito 24May90 74°45'W 05°08'S Erwin de al Colls; TSn/8; insecticidal fogging of *Scheelea* palms with epiphytes at 4 m [USNM].

Type locality.-- Cocha Shinguito, department of Loreto, Peru.

Derivation of specific epithet.-- From Latin *tres* and *punctum*, in allusion to the three discal setigerous punctures on each elytron.

Description.-- Character states of the *C. aerata* group and the following. See Tables III, V and VII for data about standardized body length, and ratios Hw/Pw and Pw/Pl.

Color. Head and pronotum rufo-testaceous; elytra piceous; appendages, antennae and mouthparts rufo-testaceous. Ventral surface of head and prothorax rufo-testaceous; mesepisternum, mesepimeron, metepisternum and metepimeron dark brunneous; metasternum darkened slightly laterally; all abdominal sternites dark brunneous laterally, broadly rufo-testaceous medially (elytral epipleuron dark brunneous).

Fixed setae. Disc of elytron with three setigerous punctures.

Elytra. Interneurs impunctate.

Male genitalia. Unknown.

Notes about habitat.-- The type specimen was taken from *Scheelea* palms with epiphytes at 4 m by fogging with an insecticide.

Geographical distribution (Map. 20).-- This species is known only from the type locality in northern Peru.

Chorological affinities.-- The type locality of this species is broadly overlapped by the range of *C. nitidula*.

Phylogenetic relationships.-- The position of this species is unresolved due to the lack of a male specimen.

Material examined.-- Type material only, see above for details.

Appendix B

James K. Liebherr, one of the reviewers of the penultimate draft of the manuscript on which this paper is based, undertook a numerical cladistic analysis of the data in Table XII, using the program Hennig 86, with the mhennig tree finding option. With Dr. Liebherr's written permission and encouragement (in his signed review of the manuscript), and to make our data more readily available to practitioners of current numerical cladistic techniques, we present, as Figs. 41A and 41B the two shortest cladograms that he found. Each of these is 239 steps, which is 12 steps or 5 per cent shorter than the 251 steps of the reconstructed phylogeny illustrated in Fig. 36.

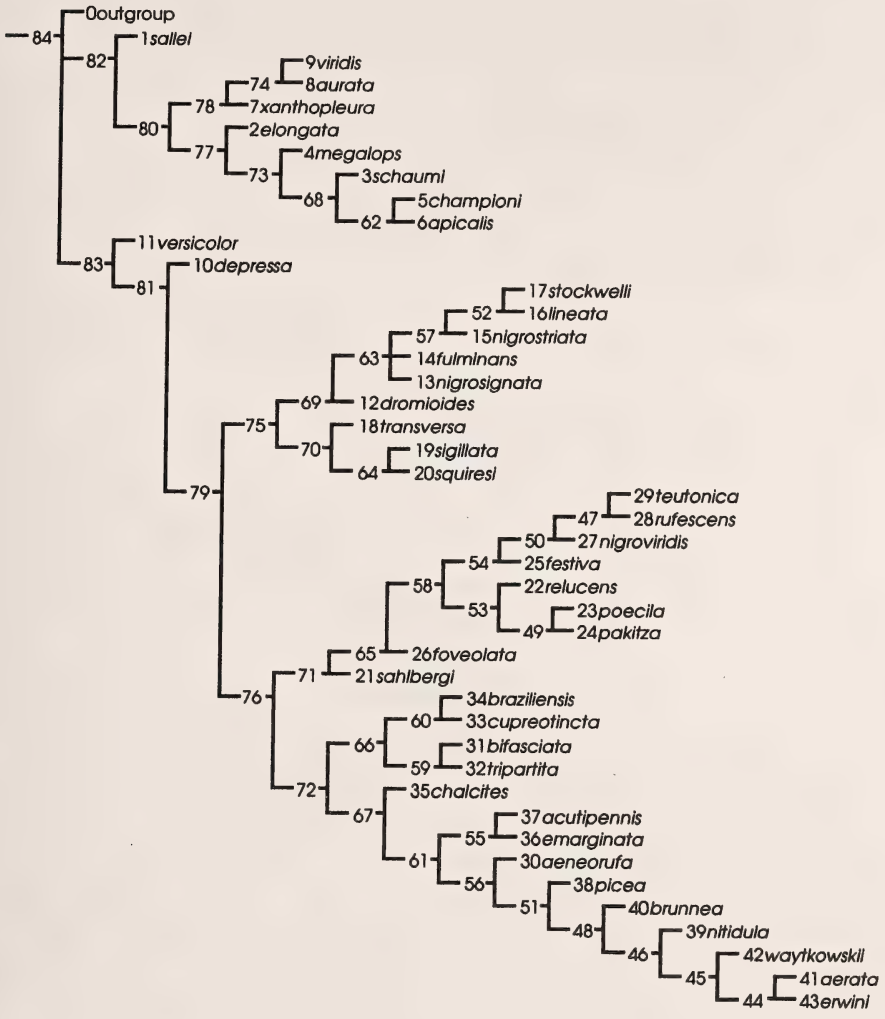

FIGURE 41A,B. The two minimum length cladograms produced by the program Hennig86, mhennig option.

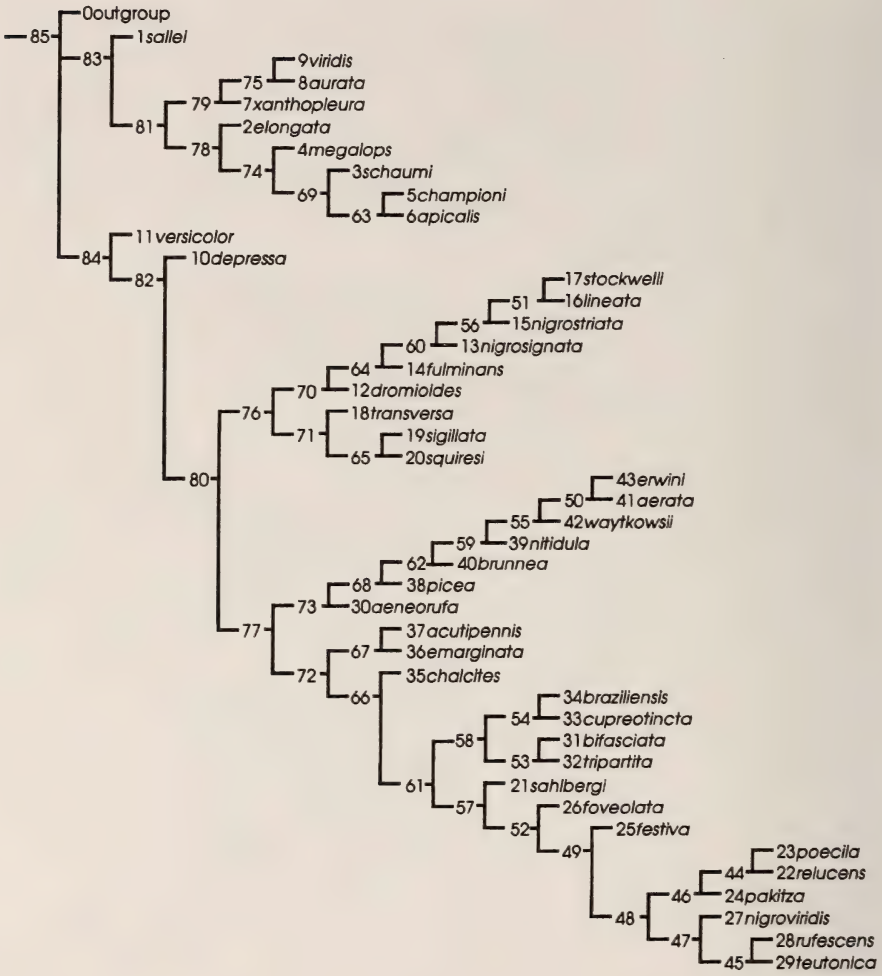

FIGURE 41A, B. - continued.

EFFECT OF PYRETHROID APPLICATIONS ON THE SEX RATIO OF THE TWOSPOTTED SPIDER MITE, *TETRANYCHUS URTICAE* KOCH (ACARINA: TETRANYCHIDAE) IN AN APPLE ORCHARD

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Abstract *Proc. ent. Soc. Ont.* 124: 183-188

The effect of pyrethroid applications on the adult sex ratio of the twospotted spider mite, *Tetranychus urticae* Koch, was studied in an apple orchard. Overall adult abundance of *T. urticae* was positively associated with pyrethroid applications. Significantly ($P < 0.05$) lower proportions of females were found in the pyrethroid treated trees than in the untreated controls. However, no significant differences in the sex ratio were found between two rates of pyrethroid applications. The reasons for the sex ratio alteration following pyrethroid applications in the field is discussed.

Introduction

An adult sex ratio of approximately 75% (proportion females in the adult population) appears to be the norm in the twospotted spider mite, *Tetranychus urticae* Koch (Wrensch 1985), although Boudreaux (1963) stated that there is no "normal" sex ratio for spider mites. Both intrinsic and extrinsic factors may affect sex ratio variability in spider mites, namely: the amount of sperm transferred to a female (Overmeer 1972), genetic factors (Overmeer and Harrison 1969), food quality and population density (Wrensch and Young 1978), maternal age and density (Li and Harmsen 1993), female age at mating (Krainacker and Carey 1990), pyrethroids (Iftner and Hall 1984), and predation by predatory mites (Johnson and Proctor 1991). Most previous studies on the sex ratio of spider mites have been done under either laboratory or controlled greenhouse conditions. In the field, however, the situation becomes more complex, and many interacting factors may be involved in establishing the sex ratio of spider mites. Although some factors, such as dispersal, predation and weather conditions are of obvious importance in influencing the sex ratio in the field, few studies have been reported in the literature. Johnson and Proctor (1991) first demonstrated that predation by phytoseiid mites in apple orchards altered the sex ratio of the European red mite, *Panonychus ulmi* (Koch), favouring females.

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It is well documented that the use of pyrethroids against major insect pests in deciduous fruit orchards is associated with outbreaks of phytophagous mites. Many reports conclude that the major cause of such outbreaks is the decimation of predatory mites by pyrethroids. However, recent studies have demonstrated that pyrethroids may also have a direct effect, enhancing the population growth rate of some phytophagous mite species (Penman and Chapman 1988; Gerson and Cohen 1989). Since these various pyrethroid based phenomena may affect males and females differently, it is reasonable to expect an overall effect on the sex ratio of tetranychid populations. In this study we examined the effect of pyrethroid insecticide applications on the sex ratio of a natural population of *T. urticae* in an apple orchard.

Materials and Methods

Field experiments were conducted in an apple orchard at the Smithfield Experimental Farm, Agriculture Canada, Trenton, Ontario. Three treatments were used during the study: two with different rates of the pyrethroid lambdacyhalothrin (50 EC, ICI Chipman, Ont.) and one with water as control. The rates of the pyrethroid used in the study were 1.25 g (AI)/ha (10% of the recommended rate of 12.5 g (AI)/ha) and 2.5 g (AI)/ha (20% of the recommended rate). Three applications of the pyrethroid were made using a hydraulic handgun on 28 June, 28 July and 31 August 1989, respectively. The orchard was divided into 24 plots of 5-7 trees each. Each plot served as a replicate, and each of the three treatments was replicated eight times. Leaf samples were taken biweekly from mid-June to the end of September. Ten intermediate-aged leaves from each tree were randomly selected from all quadrants of the tree canopy up to 2 m above the ground (Li and Harmsen 1992). The population density of *T. urticae* was estimated from counts of individual mites on both sides of the leaves, with the aid of a dissecting microscope in the laboratory. The number of adult males and females were recorded separately. The data were transformed as $\sqrt{x + 0.5}$ and subjected to analysis of variance (ANOVA) (Zar 1984), where x is the number of adults per 10 leaves from each tree. Sex ratio was evaluated as the proportion of females (%) = females/(females + males) * 100%, and the data were transformed as $\arcsin\sqrt{P}$ before ANOVA (Zar 1984), where P is the proportion of females. Significant differences in the sex ratio were compared among the three different treatments within each sample date, and separated by Duncan's multiple range test at $P = 0.05$ level.

Results

Effect of pyrethroid applications on the abundance of adult *T. urticae*

The mean density of adult *T. urticae* increased significantly after pyrethroid applications in the field (Fig. 1). From 27 July to 26 September, the counts of adults in the pyrethroid treated trees were significantly ($P < 0.05$) higher than in the untreated ones. The population density of adults increased with the pyrethroid rates, but the differences between the two pyrethroid treatments were not significant except for the 29 August sample. On average, 44.6±4.7 (mean±SE), 29.7±3.5 and 4.2±0.9 adults were found in the 1.25 g (AI)/ha, 2.5 g (AI)/ha and water sprayed trees on the 29 August sample, respectively.

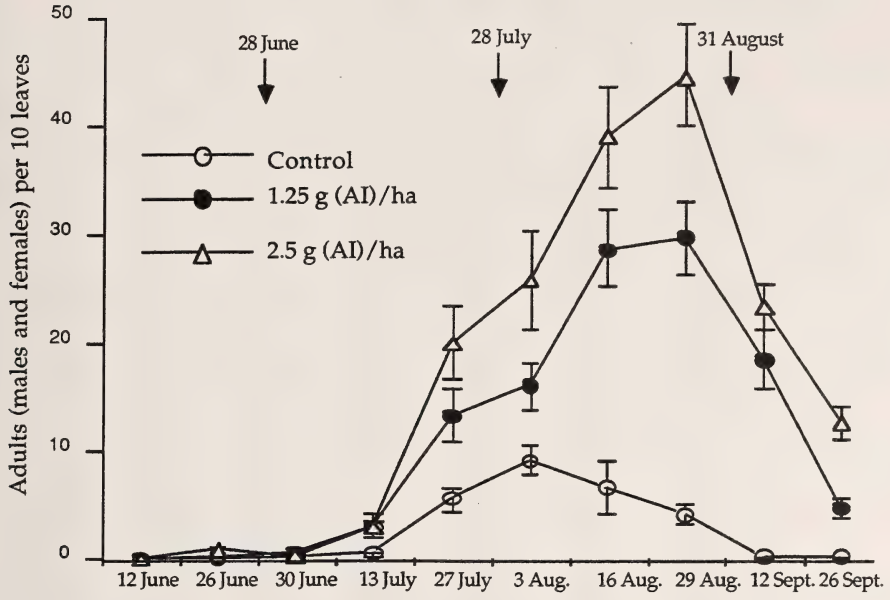

FIGURE 1. Mean density of adults *T. urticae* in different treatment trees following pyrethroid (lambdacyhalothrin) applications in an apple orchard. Vertical bars indicate standard errors of mean. Arrows indicate time of the pyrethroid applications.

Effect of pyrethroid applications on the sex ratio of *T. urticae*

The sex ratio of *T. urticae* was significantly altered following pyrethroid applications in the field (Fig. 2). A lower proportion of females was associated with pyrethroid applications, suggesting differential effect of pyrethroid applications on the incidence of adult males and females. The differences were significant ($P < 0.05$) in five of seven samples. In the trees treated with two different rates of the pyrethroid, the female proportion had almost equal values, indicating that saturation was reached with the lower rate of the pyrethroid.

Discussion

The population density of adult *T. urticae* was dynamic (Fig. 1), but the sex ratio appeared to be no major changes over the season in the field (Fig. 2), suggesting that there is no relationship between the sex ratio and overall population density as found by Herbert and Butler (1975) in an apple orchard population of *P. ulmi.* An overall female proportion of 77.9% was found in this study.

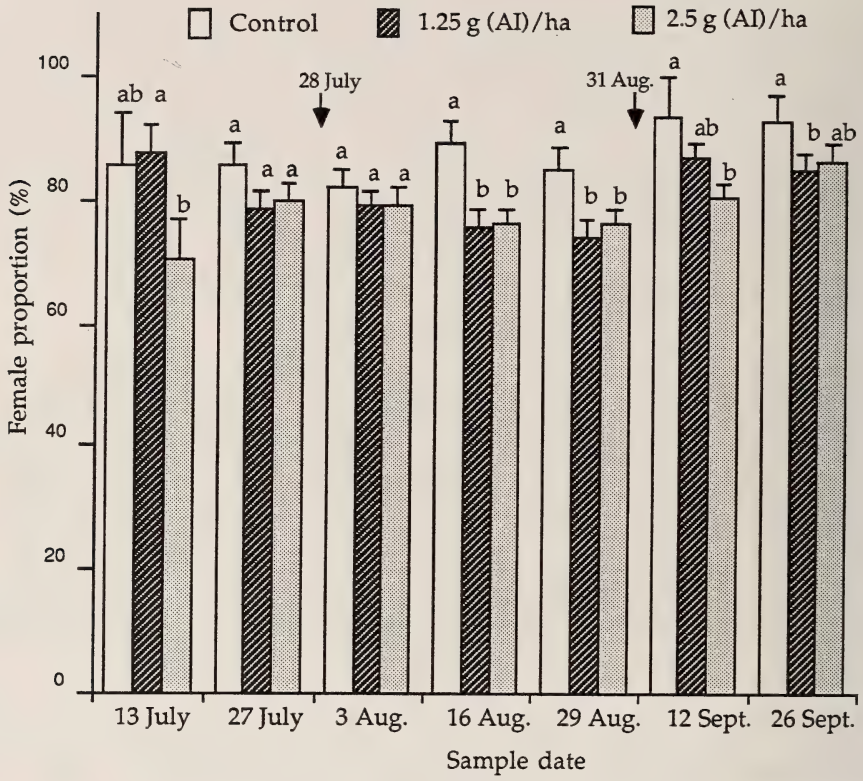

FIGURE 2. The sex ratio (female proportion) of adult *T. urticae* in different treatment trees following pyrethroid (lambdacyhalothrin) applications in an apple orchard. Arrows indicate time of the pyrethroid applications. Vertical bars indicate standard errors of mean. Bars with the same letters within the sample date indicate that female proportion are not significantly different ($P > 0.05$, Duncan's multiple range test).

Our data show that adult *T. urticae* density increased and female proportion decreased following pyrethroid applications in the field. This agrees with what Johnson and Proctor (1991) reported on *P. ulmi* following carbaryl spray. However, our results contrast with the findings of Iftner and Hall (1984). They reported that *T. urticae* produces higher proportion of daughters on bean leaves treated with fenvalerate (a pyrethroid) than on control leaves. There are several possible explanations for the sex ratio change following insecticide applications. Johnson and Proctor (1991) concluded that the main reason is predation by predaceous mites, and hypothesized that the more active adult males have a greater chance to be preyed upon than adult females. Clements and Harmsen (1990) found that the stigmaeid *Zetzellia mali* (Ewing) does not prey on adult prey mites, and that phytoseiids prefer immature prey stages over adults. *Z. mali* consisted of more than 50% of the total population of predatory mites in our research orchard (Li and

Harmsen 1992). Therefore, the possibility for adult *T. urticae* to be preyed upon by predaceous mites seems to be relatively low in the orchard. Even though phytoseiid predators do prefer adult males over adult females of *T. urticae* under laboratory conditions (Clements and Harmsen 1990), the chance of adults to be preyed is much smaller than that of immature stages. Hence, predation by predatory mites may not be as an important factor affecting adult sex ratio of *T. urticae* as other factors in this study, such as dispersal behaviour.

Experiments show that females disperse from their natal area after mating (Mitchell 1973). Smitley and Kennedy (1985) reported that adult females of *T. urticae* exhibit aerial dispersal posture if sufficient wind is present, but adult males do not have such an aerial dispersal posture. Pyrethroid insecticides have been shown to stimulate dispersal of spider mites from treated foliage (Margolies and Kennedy 1988; Penman and Chapman 1988; Gerson and Cohen 1989) due to repellent effect on mobile stages (Iftner and Hall 1983). The low rates (10-20% of the recommended rate) used in this study may stimulate females of *T. urticae* to adopt the aerial dispersal posture, and then wind will help these individuals to disperse from the treated area to other parts of the orchard. Such differential dispersal behaviour of *T. urticae* adults is a likely cause of the observed effect. Even small changes in sex ratio and within orchard dispersal can have major effects on pest population dynamics, especially when the pest and predator populations are near equilibrium thresholds. The effects of low rate insecticide applications on mite sex ratio may have to be taken into account in the use of forecasting methods and the design of integrated pest management protocols.

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FIELD WEIGHTS OF JACK PINE BUDWORM LARVAE (LEPIDOPTERA: TORTRICIDAE) SURVIVING AERIAL APPLICATIONS OF *BACILLUS THURINGIENSIS* AND TWO CHEMICAL INSECTICIDES

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Abstract *Proc. ent. Soc. Ont.* 124: 189-196

Commercial formulations of *Bacillus thuringiensis* (*B.t.*) (Futura XLV), aminocarb (Matacil 180F) and fenitrothion (Sumithion 20F) were applied aerially at 20 and 30 BIU/ha, 2 x 70 g and 2 x 210 g/ha, respectively against jack pine budworm *Choristoneura pinus pinus* Freeman (Lepidoptera: Tortricidae) in stands of 25- to 35-year old jack pine *Pinus banksiana* Lambert. Larvae that survived *B.t.* at 30 BIU/ha in general, weighed, significantly less (P=0.05) than those that survived the aminocarb, fenitrothion and *B.t.* at 20 BIU/ha treatments. No significant differences in mean weights were observed between the surviving insects sprayed with *B.t.* at 20 BIU/ha and those that survived the synthetic chemicals. Mean seventh instar dry weights in the *B.t.*-30 BIU, aminocarb, *B.t.*-20 BIU and fenitrothion plots were 12, 26, 27 and 29% of their respective live weights. Mean dry weight of the seventh instars in the check plots was approximately 22% of their mean live weight. These findings suggest that the weights of jack pine budworm larvae that survive *B.t.* at 30 BIU/ha tend to be significantly more retarded than those that survive *B.t.*, aminocarb and fenitrothion at 20 BIU, 70 g and 210 g/ha, respectively; and that there is potential to use weights of surviving larvae as an additional criterion to assess the field efficacy of *B.t.* against jack pine budworm.

Introduction

Jack pine, *Pinus banksiana* Lambert, grows from west of the Rocky Mountains to the Atlantic regions of Canada and the United States. The jack pine budworm (JPBW), *Choristoneura pinus pinus* Freeman (Lepidoptera: Tortricidae), is considered to be the most important insect pest of jack pine in central Canada and the Lake States region of the United States (DeBoo and Hildahl 1967). Outbreaks of this species, which occur periodically and usually last 1 to 4 years, can kill or deform considerable tracts of jack pine (Clancy *et al.* 1980). In most cases the forest industry appears to be willing to tolerate losses of merchantable jack pine trees by letting the outbreaks collapse naturally, rather than applying insecticides to suppress short-lived outbreaks (Prebble 1975).

In 1985 JPBW infestations increased rapidly for the second consecutive year in northern Ontario and threatened the socioeconomic stability of some communities that depended directly or indirectly on jack pine for a livelihood. This necessitated the development of strategies to suppress the JPBW outbreak and to protect the jack pine resource (Cadogan *et al.* 1986), and presented opportunities for various JPBW field studies.

Morris (1973) and Morris and Moore (1983) postulated that the efficacy of microbial control agents in most forest situations should not be assessed on the same basis as chemical insecticides

using pest population reductions and host tree damage; but rather, the assessment criteria should be extended to include the impact of the microbials on pest longevity, pupal emergence, reproductive potential, teratological manifestations and offspring survival.

A review of the literature shows that sublethal infection by *Bacillus thuringiensis* Berliner (*B.t.*) of a number of forest insects resulted in a range of secondary effects. Among these, Angus (1965) reported on the failure of spruce budworm *Choristoneura fumiferana* (Clem.) to eclose; Morris (1973) showed that a number of forest insect species suffered weight loss after *B.t.* treatments and Smirnoff (1983) reported that spruce budworm populations that survived *B.t.* treatments were less vigorous than those that survived chemical insecticides or those that were untreated. However, none of the studies investigated JPBW.

This author supports the concept that if a treatment can demonstrate quantifiable secondary biological effects that enhance the treatment's effectiveness, these effects should be used as evaluation criteria. However, if "secondary effects" are to be considered as valid criteria for assessing the field efficacy of *B.t.* against insect pests in boreal forests, it will be necessary to delineate which effects are to be used, provide pertinent supporting data for major forest pests including JPBW and determine if the magnitude of the effects are indeed unique to *B.t.*

This paper presents results of a field study that was conducted in 1985 to determine to what extent commercial formulations of *Bacillus thuringiensis* var. *kurstaki*, fenitrothion and aminocarb affected the weights of those JPBW that survived the treatments; and to evaluate if reductions in larval weights could be used to assess the field efficacy of *B.t.* against JPBW.

Materials and Methods

Study Site

The field trial was conducted approximately 25 km southeast of Gogama in north-central Ontario, Canada. Five 50 ha blocks (1.0 x 0.5 km), one per treatment and one as a check, were selected in naturally regenerated, 25- to 35-year-old pure jack pine stands. Three 10- to 15-ha plots transected each block and 25 sample trees of uniform size (ca. 10 m tall) were selected at random in each plot.

Insecticide Application

Three commercial insecticides were used in this study. Futura XLV, a concentrated extra low viscosity formulation of *Bacillus thuringiensis* var *kurstaki* (14.4 Billion International Units (BIU)/L; 230 centipoise at 5^0C) was sprayed undiluted at 20 BIU (1.4L) and 30 BIU (2.1L) per hectare as single application treatments. Sumithion 20F (200g fenitrothion/L) and Matacil 180F (180g aminocarb/L), both aqueous flowable formulations of synthetic chemical insecticides were each sprayed at 210g AI/ha and 70g AI/ha, respectively. Sumithion and Matacil were both mixed with water [64.5:34.5 (%V/V) and 25.9:71.85 (%V/V), respectively]. Atlox 3409F, an emulsifier was added (1.25% V/V) to the Sumithion mix. Both mixes were sprayed twice at 1.5 L/ha. All three insecticides were dyed as described by Cadogan *et. al.* (1986) to facilitate deposit assessments. Erio Acid red dye (0.2% W/V) for Futura XLV and Rhodamine B red dye (1.0% V/V) for Matacil and Sumithion.

The insecticides were applied with a Cessna 188B Ag truck aircraft fitted with four AU 3000 Micronair rotary atomizers. The first application of Matacil 180F and Sumithion 20F was on June 21 and the second application on June 26. Futura XLV at 20 BIU/ha and 30 BIU/ha were sprayed on June 23 and June 25, respectively. All treatments were applied between 05:30h and 06:40h

under stable weather conditions. The aircraft flew approximately 10m above the forest canopy at 160 km/h when spraying. The chemical insecticide spray volumes were emitted at 18.3L/min., whereas the flow rates for Futura XLV at 20 BIU/ha and 30 BIU/ha were 16.7 L/min. and 25.0 L/min., respectively.

Jack pine needles were beginning to escape their fascicle sheaths and JPBW were primarily third and fourth instars when the first sprays were applied.

Sampling

JPBW populations were sampled, at ca. 5-to 7-day intervals, once before and three to four times after the spray. At each sampling, two 60-cm midcrown branch tips were taken from each sample tree using pole pruners with baskets attached (Churcher 1981) and taken to a field laboratory where they were processed. The living larvae were removed from the branches and counted (Martineau and Benoit 1973; Cadogan *et. al.* 1984). Randomly selected individual insects of various instars were immediately taken from these pools of insects, cleaned of extraneous materials (frass and plant material) and weighed, using a Mettler AC100 electronic balance. After being weighed, sixth and seventh instars were stored in 95% methyl alcohol and later taken to the Forest Pest Management Institute's laboratory in Sault Ste. Marie, where they were oven-dried (4 h at 150°C) and reweighed.

In the autumn of 1985 the sample trees (75 per treatment) were re-examined to determine the extent of defoliation. Two 60-cm branch tips were taken from each sample tree and assessed using Fettes' (1950) method, with six defoliation classes (0, 1-25, 26-50, 51-75, 76-99 and 100% damage) instead of 10. Because Fettes' method was developed primarily to evaluate the defoliation of balsam fir (*Abies balsamea* L.) and spruce (*Picea* sp.) by spruce budworm, the procedures in this study were modified slightly to accommodate jackpine/JPBW relationships. For example, because JPBW usually cut the jackpine needles laterally at their base, which results in their dessication, careful observations were required to distinguish between JPBW damage and needles that had dried from other factors.

Statistical Analysis

The data were analyzed using BMDP statistical software program 7D (Dixon 1983). The software allowed a wide range of options (ANOVA, Brown-Forsythe and Levene tests), whether the data were normally distributed or not, without employing data transformations. All hypotheses were tested at $P = 0.05$.

Results and Discussion

Table I presents data on the prespray JPBW populations and the residual populations that survived in the treatment and check areas. The spray deposits (Table I) indicate that the treatments were adequate, which suggests there was a high probability that the surviving budworm were exposed to sublethal dosages of the treatments. The levels of defoliation shown are intended to demonstrate that enough foliage remained to feed survivors and that none of the populations should have suffered from involuntary starvation due to lack of food.

Prior to the sprays, the weights of third and fourth instars in the plots varied considerably (Table II). The third instars in the plots treated with *B.t.* at 20 BIU/ha were significantly heavier than those in the other plots. Just prior to the applications, the fourth instars in both designated *B.t.* treatment plots were significantly heavier ($P = 0.05$) than those in the check plots and those

TABLE I. Insecticide spray deposit, larval jack pine budworm population changes and host tree defoliation relating to four treatments in jackpine plots near Gogama, Ontario. 1985.

Treatment - AI/ha	Number of Larvae/60 cm branch $\bar{x}$±SD		Spray deposit			% Defoliation $\bar{x}$±SD
	Prespray	Postspray[1]	Drops/cm^2 $\bar{x}$±SD	VMD µm	NMD µm	
Futura XLV - 20 BIU	15.0±12.4	7.6±4.8	5.4±6.4 a	57	12	56±22
Futura XLV - 30 BIU	10.1±19.0	2.6±2.6	8.4±6.6 a	62	16	26±23
Sumithion 20F - 210 g	20.4±30.8	2.3±2.8	8.8±3.9 a	73	29	29±21
			51.6±22.0 b	66	29	
Matacil 180F - 70 g	17.4±26.8	6.3±5.6	18.9±9.4 c	73	11	50±29
			18.0±9.8 c	73	8	
Control	15.6±17.9	13.5±10.7				77±24

[1] Taken when larvae were seventh instar.
Means followed by unlike letters are significantly different ($P = 0.05$) using BMDP comparison of means with the Bonferroni inequality (Dixon 1983)
VMD & NMD - volume & number median diameters, respectively.

plots designated for the synthetic chemicals. The author hesitates to place too much emphasis on these two observations primarily because the weights were derived from single samplings. Rapid larval development allowed only one prespray sample, and it has been shown that multiple samplings on different dates produce more reliable weight estimates of a given instar than a single sample (Table III). Failure to observe this requirement might produce invalid conclusions. Fifth instars that survived *B.t.* at 30 BIU/ha were observed to have significantly lower mean weights than other survivors, while larvae surviving the chemical treatments were similar to the control (Table II). The fifth- and seventh-instar JPBW in the plots treated with *B.t.* at 30 BIU/ha weighed significantly less than those in the control plots. However the mean weight of sixth instars in the *B.t.*-30 plots, although significantly less than two of the other treatment means, was not significantly different from the control. As the surviving larvae reached the seventh instar, only those in the 30 BIU/ha treatment were shown to exhibit a mean weight that was significantly different from the control. Whereas survivors from both *B.t.* treatments were observed to be lighter than those in the aminocarb and fenitrothion plots, the weights were not significantly different.

However, dry weights of the seventh instars treated with *B.t.* at 30 BIU/ha were dramatically less than those in the chemical or control plots (Table II). The mean dry weights of seventh instars surviving in the *B.t.*-20BIU, Sumithion, Matacil and control plots were 27, 29, 26 and 22% of their live weights respectively, compared with 12% in the *B.t.*-30 BIU plots (Table II). It might be that the conversion of food uptake to tangible tissue or biomass was reduced by consumption of sublethal dosages of this particular treatment. Morris (1973) observed that weight reductions in four Lepidoptera species intensified as the *B.t.* dosage rate increased; nevertheless, it is not clear

TABLE II. Prespray and postspray field weights of jack pine budworm in jack pine plots treated with Bt, fenitrothion and aminocarb.

Treatment AI/ha	Mean larval weight (mg)±SD										
	Prespray Instar				Postspray Instar						Pupa[2]
	n	3	n	4	n	5	n	6	n	7[1]	
Futura XLV-20 BIU	80	1.68±0.23 a	50	3.19±0.56 a	2/200	4.68±0.69 a	2/200	21.03±3.20 ac	2/79	53.19±27.3 ab 14.44±3.34*	53.41±13.65 a
Futura XLV-30 BIU	60	0.87±0.25 b	30	2.30±0.73 a	2/180	3.95±0.80 b	2/200	16.83±2.86 b	2/91	48.23±26.22 a 5.90±2.40 ∓	----
Sumithion 20F-210g	150	0.51±0.16 b	50	1.38±0.20 b	4/270	5.95±1.68 a	3/200	23.70±7.33 ac	3/107	56.47±28.20 ab 16.62±3.39*	58.42±20.91 a
Matacil 180F - 70g	100	0.66±0.16 b	50	1.21±0.13 b	3/210	5.34±1.75 a	3/290	23.10±3.33 ac	2/79	60.02±29.66 ab 15.74±2.76*	----
Control	100	1.08±0.15 b	50	1.29±0.23 b	3/200	4.89±1.14 a	3/200	19.71±3.11 bc	3/121	64.28±27.66 b 13.89±2.69*	57.81±14.56 a

[1] Upper & Lower figures denote live & dry weights that are analyzed separately.

[2] The same ♀ : ♂ for each treatment; --- indicate insufficient numbers for statistical treatments.

n Number of samplings/number of individuals.

Means in a column followed by unlike letters or symbols are significantly different (P=0.05) using BMDP comparisons of means with the Bonferroni inequality (Dixon 1983).

TABLE III. Live weights of larval jack pine budworm at different samplings after *B.t.* and chemical insecticides' sprays.

Instar	Sampling sequence	Mean larval weights (mg)±SD				
		Treatment				
		Futura XLV - 20	Futura XLV - 30	Sumithion - 210 g	Matacil - 70 g	Control
5	1	4.3±0.5	3.6±0.8	7.6±0.9	7.6±1.1	6.2±0.9
	2	4.9±0.6	4.3±0.5	5.0±1.0	4.3±1.3	4.2±0.5
	3			4.0±0.7	4.2±0.6	4.3±0.4
	4			5.7±1.2	5.3 ±1.1	
6	1	20.8±3.7	17.8±3.1	19.5±8.1	20.9±2.8	20.8±2.3
	2	21.2±2.7	15.9±2.4	21.9±3.3	22.8±2.9	20.8±2.5
	3			29.6±7.5	25.8±2.6	14.5±2.6
7	1	47.5±24.9	45.7±23.7	32.4±9.4	32.2±9.2	44.9±20.1
	2	58.6±28.7	50.3±28.2	54.4±22.9	52.5±27.4	68.4±28.4
	3			73.1±29.5	77.6±25.8	70.7±29.5

why this reduction in dry weight differed so significantly from *B.t.* at 20 BIU/ha. The concentration of active ingredient in a spray drop of a given diameter from both *B.t.* treatments was constant and the data for deposit taken at ground level (Table I) indicate that there was no significant difference between these two treatments. Nevertheless, it could have been that there were significantly different sublethal dose acquisitions by larvae in the two treatments. Fifth, sixth, and seventh instars in plots treated with Matacil 180F and Sumithion 20F in most cases weighed more, though not always significantly so, than those in plots treated with *B.t.* or those in the untreated control plots (Table II). Considering that the weights of prespray larvae in the plots treated with the chemical insecticides were generally less than those in the other plots, these results suggest that exposure of JPBW larvae to sublethal dosage of aminocarb and fenitrothion does not retard larval weight gain.

Although post-treatment larval weights in the *B.t.* plots were not always statistically lower than those in the other plots, the overall indications are that *B.t.* at 30 BIU/ha has a higher potential to retard JPBW larval weights than the chemical insecticide treatments. Moreover, we need to emphasize the significance and potential impact of biological differences rather than their statistical status.

Statistically acceptable numbers of pupae of both sexes ($n \geq 25$) were collected only in plots treated with *B.t.*-20, fenitrothion and in the control plots. The mean weights of these pupae were shown to be not significantly different (Table II).

The sporadic nature of JPBW epidemics has precluded, to date, further studies to corroborate these findings. Nevertheless, it is expected that continuing studies will further elucidate the interactions between insecticides such as *B.t.*, and *Choristoneura pinus pinus*. If larval weights are to be used routinely as a criterion to assess *B.t.* efficacy against this species, it will be especially

necessary to explore and document how larval weights affect JPBW populations. For example, although it has been shown with the genus *Choristoneura* Led. that fecundity is strongly correlated with pupal weight (Campbell 1962; Harvey 1983) and pupal size (Miller 1957), we will still need to know the relationships between JPBW larval weight reductions induced by *B.t.* and the reproductive capabilities of the resultant adult moths; and how these are involved in the resurgences of JPBW populations. However, this study has shown that although fenitrothion suppressed JPBW populations satisfactorily, neither of the chemical insecticides affected the weights of surviving JPBW larvae; whereas *B.t.* affected larval weights only when the treatment effectively controlled the JPBW populations. Thus it is evident that there is potential to use larval weights as an additional criterion to assess the field efficacy of *B.t.* against *C. pinus pinus*.

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A CATALOGUE OF TYPES OF MISCELLANEOUS TERRESTRIAL ORDERS IN THE CANADIAN NATIONAL COLLECTION OF INSECTS (ARTHROPODA: INSECTA), INCLUDING AMBER FOSSILS.

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Abstract *Proc. ent. Soc. Ont.* 124: 197-207

This catalogue presents data about the type material of the miscellaneous terrestrial orders of arthropods housed in the Canadian National Collection of Insects, Ottawa, Ontario (CNC). Information is provided on 110 holotypes, 45 allotypes, 1 neotype, and 1 lectotype in the following groups: Collembola, Mallophaga, Mecoptera, Megaloptera, Neuroptera, Orthoptera, Notoptera and Siphonaptera. Data on the types of amber fossil taxa in the CNC are also included.

Introduction

The International Commission of Zoological Nomenclature (1985, recommendation 72 G(5)) recommended that institutions in charge of natural history specimens publish a list of type material in their care. This paper has been prepared in order to comply with this recommendation, to assist workers in other institutions in locating type material, and to stimulate further work. Catalogues of type specimens in the Canadian National Collection have been prepared for Coleoptera (de Ruette, 1970; McNamara 1977, 1984, 1993), Diptera (Cooper 1991 and Cooper & Cumming 1993) and Hymenoptera (Sarazin 1985, 1986a,b,c, 1987a,b). Locality data is shown as written on the original label. Brackets [ ] indicate information not shown on the original label. Host names are included where deemed necessary. Sex of type is shown when available in the original publication or on the label. Included herein are data on 110 holotypes, 45 allotypes, 1 neotype, and 1 lectotype in the following groups: Collembola, Mallophaga, Mecoptera, Megaloptera, Neuroptera, Orthoptera, Notoptera and Siphonoptera. Fossils in amber include 13 holotypes and 2 allotypes.

Collembola

Agrenia agilis Fjellberg 1986, Entomologica Scandinavica, 17:101.

Holotype: Canada. Garibaldi Park, B. C. Black Tusk Meadows, 2.IX.1983. Wet moss in brook, 1.710 m. 405/83. A. Fjellberg. CNC No. 21203.

Agrenia atroviridis Fjellberg 1986, Entomologica Scandinavica, 17:104.

Holotype: Canada. Garibaldi Park, B. C. 2.IX.1983 Helm Glacier. On muddy ice. 398/83. A. Fjellberg. CNC No.21204.

Agrenia cyanura Fjellberg 1986, Entomologica Scandinavica, 17:102.
Holotype: Canada King Creek, Kananaskis, Alb. 3.VII.1983 Moss in spray along waterfall. 222/83. A. Fjellberg. CNC No. 21205.
Agrenia polymorpha Fjellberg 1986, Entomologica Scandinavica, 17:96.
Holotype: ♂ Canada Kananaskis Alb. Marmot Creek, 27.VI.1983 Wet moss on stones. 2.030 m. 184/83. A. Fjellberg. CNC No.21206.
Agrenia riparia Fjellberg 1986, Entomologica Scandinavica, 17:103.
Holotype: NORWAY STI: Melhus Kvål, 8.XII.1984 At Gaula. O. Hanssen leg. CNC No. 21207.
Anurida decemoculata Hammer 1953, Acta Arctica, 6:29.
Holotype: Canada 1948 [N. W. T.] Reindeer St[ation]. 163. M. Hammer. CNC No. 18192.
Ceratophysella gibbomucronata Hammer 1953, Acta Arctica, 6:17.
Holotype: Canada 1948 [N. W. T.] Reindeer St[ation]. 160. M. Hammer. CNC No. 18186.
Ceratophysella glancei Hammer 1953, Acta Arctica, 6:18.
Holotype: Canada 1948 [N. W. T.] Coppermine 205. M. Hammer. CNC No. 18187.
Deuterosminthurus undulatus Hammer 1953, Acta Arctica, 6:59.
Holotype: Canada 1948 [N. W. T.] Reindeer St[ation]. 87. M. Hammer. CNC No. 18200.
Entomobrya lateropicta Hammer 1953, Acta Arctica, 6:54.
Holotype: Canada 1948 [N. W. T.] Yellowknife 332. M. Hammer. CNC No. 18199.
Entomobrya ontarionensis James 1933, Transactions of the Royal Canadian Institute, 19:79.
Holotype: Pottageville Ont. 22-III-1931, H. G. James. CNC No. 3717.
Folsomia duodecimesetosa Hammer 1953, Acta Arctica, 6:48.
Holotype: Canada 1948 [Manitoba] Churchill 486. M. Hammer. CNC No. 18198.
Isotoma multispinata James 1933, Transactions of the Royal Cananadian Institute, 19:111.
Holotype: Rondeau Park Ont. 2-VIII-1931, H. G. James. CNC No. 3738.
Lepidocyrtus unifasciatus James 1933, Transactions of the Royal Canadian Institute, 19:107.
Holotype: Rondeau Park Ont. 3-VIII-1931 H. G. James. CNC No. 3737.
Mackenziella psocoides Hammer 1953, Acta Arctica, 6:60.
Holotype: Canada 1948 [N. W. T.] Reindeer St[ation]. 53. M. Hammer. CNC No. 18201.
Micranurida papillosoides Hammer 1953, Acta Arctica, 6:28.
Holotype: Canada 1948 [N. W. T.] Coppermine 295. M. Hammer. CNC No. 18191.
Micranurida spirillitera Hammer 1953, Acta Arctica, 6:25.
Holotype: Canada 1948 [N. W. T.] Yellowknife 384. M. Hammer. CNC No. 18190.
Morulina mackenziana Hammer 1953, Acta Arctica, 6:32.
Holotype: Canada 1948 [N. W. T.] Reindeer St[ation]. 67. M. Hammer. CNC No. 18194.
Morulina thulensis Hammer 1953, Acta Arctica, 6:31.
Holotype: Canada 1948 [Manitoba] Churchill 486. M. Hammer. CNC No. 18193.
Neogastrura macrotuberculata Hammer 1953, Acta Arctica, 6:13.
Holotype: Canada 1948 [N. W. T.] Reindeer St[ation]. 132. M. Hammer. CNC No. 18185.
Onychiurus aborigensis Fjellberg 1987, Entomologica Scandinavica, 18:285.
Holotype: ♀ USSR: Magadan Reg. Aborigen. 27.VII.1979. A. Fjellberg leg. CNC No. 20102.
Onychiurus alnus Fjellberg 1987, Entomologica Scandinavica, 18:282.
Holotype: ♀ USSR: Magadan Reg. Aborigen 27.VII.1979. A. Fjellberg leg. CNC No. 20108.
Onychiurus churchilliana Hammer 1953, Acta Arctica, 6:44.
Holotype: Canada 1948 [Manitoba] Churchill 572. M. Hammer. CNC No. 18197.

Onychiurus interruptus Fjellberg 1987, Entomologica Scandinavica, 18:282.
Holotype: ♀ USSR: Magadan Reg. "Death Valley", Magadan-Ust UmZug 209 km from Magadan 30.VII.1979. A. Fjellberg leg. CNC No. 20107.
Onychiurus macrodentatus Hammer 1953, Acta Arctica, 6:43.
Holotype: Canada 1948 [N. W. T.] Reindeer St[ation]. M. Hammer. CNC No. 18196.
Onychiurus nataliae Fjellberg 1987, Entomologica Scandinavica, 18:281.
Holotype: ♂ USSR: Chukotka Chaun Bay. 13.VIII.1977, S. F. MacLean leg. CNC No. 20114.
Onychiurus nudus Fjellberg 1987, Entomologica Scandinavica, 18:283.
Holotype: ♀ Alaska Canning River Delta. 26.VII.1980. S. F. MacLean leg. CNC No. 20103.
Onychiurus paucisetosus Hammer 1953, Acta Arctica, 6:42.
Holotype: Canada 1948 [N. W. T.] Reindeer St[ation]. 7. M. Hammer. CNC No. 18195.
Onychiurus pingicolus Fjellberg 1987, Entomologica Scandinavica, 18:285.
Holotype: ♂ Alaska Prudhoe Bay 16.VIII.1976. A. Fjellberg leg. CNC No. 20099.
Onychiurus reversus Fjellberg 1987, Entomologica Scandinavica, 18:287.
Holotype: ♀ Alaska Canning River Delta 23.VII.1980. S. F. MacLean leg. CNC No. 20098.
Paranura quadrilobata Hammer 1953, Acta Arctica, 6:24.
Holotype: Canada 1948 [N. W. T.] Reindeer St[ation]. 10. M. Hammer. CNC No. 18189.
Proisotoma similis James 1933, Transactions of the Royal Canadian Institute, 19:87.
Holotype: Belleville, Ont. 18-V-31. H. G. James. CNC No. 3716.
Xenylla canadensis Hammer 1953, Acta Arctica, 6:20.
Holotype: Canada 1948 [N. W. T.] Yellowknife 395. M. Hammer. CNC No. 18188.
Xenylla pseudomaritima James 1933, Transactions of the Royal Canadian Institute, 19:87.
Holotype: Chatham Ont. 28-VII-31. H. G. James. CNC No. 3736.
Xenyllodes wapiti Fjellberg 1985, Entomologica Scandinavica, 16:131.
Holotype: Canada. Saskatchewan: Cypress Hills S of Maple Creek. 5.VI.1983./Litter in rich aspen forest. A. Fjellberg leg. CNC No. 19044.

Mallophaga

Lagopoecus gibsoni Hopkins 1946, Annals and Magazine of National History Ser. 11, 13:170.
Holotype: Dollard, Sask. 10.VII.1935, C. F. Holmes.
Allotype: same data as holotype. Host: *Centrocercus urophasianus* (Bonaparte). CNC No. 5693.
Trichodectes pinguis euarctidos Hopkins 1954, Entomologist, 87:142.
Holotype: ♂ Gray Crk. B. C. 3 June 1936.
Allotype: ♀ same data as holotype. Host: *Euarctos americanus* (Pallas). T. K. Molliet. CNC No. 21208.

Mecoptera

Boreus reductus Carpenter 1931, Bulletin of the Museum of Comparative Zoology, 72:241.
Holotype: Kaslo B. C. XII-29-1906. CNC No. 3450.
Allotype: same as holotype.

Neopanorpa chillcotti Byers 1971, Journal of the Kansas Entomological Society, 44:4.
Holotype: ♂ Nepal, Ktmd. Godavari, 5000' 31.VII.1967.
Allotype: ♀ Nepal, Ktmd. Godavari, 6000' 24 July 1967. Can. Nepal Exped. CNC No. 12991.

Megaloptera

Protochauliodes spenceri Munroe, Canadian Entomologist, 85:190.
Holotype: ♂ Duncan B. C. 28.VI.1918, W. Downes.
Allotype: ♀ Langford B. C. 1.VIII.51. In flight. D. Evans. CNC No. 6002.

Neuroptera

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1993 ANNUAL MEETING

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1994

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"Will you walk into my parlor?
Said the spider to the fly;
'Tis the prettiest little parlor
That ever you did spy;
You only have to pop your head
Just inside of the door,
And you'll see so many curious things
You never saw before."

From: Fyles, T. W. 1894
Volume 25: 49-56

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DEVELOPMENT OF SPRING *AEDES* MOSQUITOES IN THREE DIFFERENT HABITATS IN RELATION TO PLANT PHENOLOGY

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Abstract *Proc. ent. Soc. Ont.* 125: 1-11

Phenological stages of 63 herbaceous plants, trees, and shrubs were monitored over three years to predict time of treatment (*ca.* third instar) for spring *Aedes* species mosquitoes inhabiting woodland, open field and cedar bog pools near Guelph, Ontario. Sixteen different species of plants proved reliable indicators for the presence of third instar larvae for one or more of the six *Aedes* species studied, despite a difference of over two months in hatching times over the three years. The combined results for all mosquitoes studied indicated that the first leaf Raspberry, *Rubus idaeus* L., could be used to predict the presence of third instar mosquito larvae for four of the five mosquito species inhabiting the woodland and open field pools. The first leaf of Lilac, *Syringa vulgaris* L., could be used to predict the presence of third instar larvae for five of six mosquito species inhabiting the cedar bog.

Introduction

Associations between plants and larvae of mosquitoes have been studied intensely, but the use of plant development (e.g. flowering) to forecast development and emergence of mosquitoes has seldom been documented in the scientific literature (Penfound *et al.* 1945). Penfound *et al.* (1945) studied the phenology of aquatic plants surrounding water reservoirs in reference to timing of malaria control in Alabama. Many ecological studies of mosquitoes have included phenological components. In Europe and Asia, Brummer-Korvenkontio *et al.* (1971), Sheremet (1974), Ryazantseva (1977), Lumiaho and Itamies (1979) and Mykahob (1980) have used phenology as a descriptive term to characterize habitat associations for various mosquito species but not for predicting development. In Canada, Bourassa *et al.* (1976) and Maire *et al.* (1978) have investigated the association of immature mosquitoes with the vegetation surrounding larval habitats, but no attempts were made to associate mosquito development with plant phenology.

Phenology of flowering plants has been used to predict emergence or egg hatch of a number of agricultural and forest pests including: the alfalfa leafminer, *Agromyza frontella* (Rondani) (Alicandro and Peters 1980); bark beetles (Kapler 1967); European corn borer, *Ostrinia nubilalis* (Hubner) (Straub and Huth 1976); European chafer, *Rhizotrogus majalis* (Razoumowsky) (Tashiro

and Gambrell 1963); oyster shell scale, *Lepidosaphes ulmi* (L.) and alfalfa weevil, *Hypera postica* (Gyllenhal) (Conrad 1972).

This paper investigates the feasibility of using phenological indicators to assist in determining the developmental stages of spring *Aedes* mosquitoes in three habitat types. In Ontario, municipal control programs and attempts by homeowners to control larval mosquitoes may be less effective or cancelled because surveying and mapping of breeding sites were not initiated at the proper time; larvae were often nearing pupation when surveys were conducted.

The phenological stages of 63 plants, shrubs or trees were examined to determine if the development of certain plant species accurately correlated with mosquito development. This would provide municipal control personnel and homeowners with simple, inexpensive indicators which could assist in determining when larval mosquito surveys and treatment programs should be initiated.

Materials and Methods

1. **Habitats** - Three larval habitats for spring *Aedes* species located approximately 8 km southeast of Guelph, Ontario were chosen for phenological studies. The pools were located within 2 km of one another. The first pool, denoted "woodland pool", was located within a deciduous wood. The pool was 4-5 ha in area with a leaf litter bottom. Depth of the water within the pool during the period of sampling ranged from 11 to 45 cm. The most abundant species of shrubs and trees within and surrounding the pool included Sugar maple, *Acer saccharum* Marsh.; Silver maple, *Acer saccharinum* L.; Red maple, *Acer rubrum* L.; Manitoba maple, *Acer negundo* L.; Red osier dogwood, *Cornus stolonifera* Michx.; Pin cherry, *Prunus pensylvanica* L.F.; Hawthorn, *Crataegus* spp.; Elm, *Ulmus americana* L.; Common buckthorn, *Rhamnus cathartica* L.; Speckled alder, *Alnus rugosa* (Du Roi); Beech, *Fagus grandifolia* Ehrh.; Trembling aspen, *Populus tremuloides* Michx.; Black willow, *Salix nigra* Marsh.; Pussy willow, *Salix discolor* Muhl. and Red pine, *Pinus resinosa* Ait.

The second pool, denoted "open field pool", was situated in a farm field that had lain fallow for several years. The substrate consisted of grass with scattered leaf litter. The pool covered approximately 3 ha and depth within the pool ranged between 8-30 cm during the period of sampling. Species of grass included Barnyard grass, *Echinochloa crusgalli* (L.) Beauv.; Brome grass, *Bromus* spp. and Quack Grass, *Agropyron repens* (L.) Beauv. Meadow willow, *Salix gracilis* L.; Pussy willow; Red osier dogwood; and Elm were scattered about the pool. All shrubs were less than 1.2 m in height.

The third pool, located in a cedar bog, covered approximately 0.25 ha and ranged in depth from 7-50 cm during the sampling period. Its substrate consisted of bare, loose-packed soil with small patches of leaf litter. The predominant plant species within and surrounding the bog was Eastern white cedar, *Thuja occidentalis* L. In addition, Black ash, *Fraxinus nigra* Marsh.; Raspberry, *Rubus idaeus* L.; Trembling aspen and Elm were present along the margins of the cedar bog.

2. **Phenological Indicators** - When choosing plants as phenological indicators the following criteria were used. Indicator species had to be common throughout southern Ontario. Plants chosen as indicators had to be easily recognized by the layperson (e.g. municipal mosquito abatement personnel and home owners). The key period to survey and implement control measures for spring *Aedes* larvae is April and May in southern Ontario. The appearance of the first leaf and first bloom were chosen to be the phenological indicator characters for the plants

surveyed. First leaf was interpreted as that period from 1 to 3 days directly after budbreak, when newly formed leaves unfurled. The second indicator used was first flower bloom, considered to be that period from 1 to 3 days when flowers opened.

In the spring of 1980, 63 herbaceous plants, shrubs and trees within a 5 km radius of the pools were observed for date of first leaf or first bloom. During 1981 and 1982 the numbers observed were gradually reduced to include the most reliable indicator species. Indicator plants were observed in open, wholly shaded, northern, southern, eastern and western exposures. Each exposure type (e.g. northern) was replicated five times. A minimum of 10 plants per exposure were observed. The period of first leaf or first bloom of all the individuals of a species from all the locality types were recorded. These were then averaged and mean date for first leaf or first bloom determined. The range of days around the mean was also recorded for each species. In this way an attempt was made to account for local differences in micro-climate that may have affected dates of first leaf and bloom.

3. **Larval Sampling** - Three collecting methods were used to sample mosquito larvae and pupae. These included 10 invertebrate cone traps, a 9-litre plastic pail (Westwood *et al.* 1983; Helson and Surgeoner 1986, Westwood and Surgeoner 1991) and three 0.05 m^2 "Belleville" or area samplers (Roberts and Scanlon 1979). Pools were sampled once every 3 days from initial egg hatch until the disappearance of pupae. The developmental stage (e.g. instars and pupae) for each species of mosquito from each pool was calculated. Plants were considered to be reliable indicators if the date for the key stage of mosquito development fell within the range of days around the mean recorded for that plant species in all three years of the study. Larvae were identified using the keys of Wood *et al.* (1979).

Wills and Fish (1973) suggested that the optimal time for control of *Aedes canadensis* (Theobald) and *Aedes excrucians* (Walker) was when larval populations consisted of 80 per cent third and 20 per cent fourth instar larvae. For the purpose of this study the optimum time for larval survey and control was considered to be that period when 80 to 100 per cent of the larval population was in the third instar. This would provide abatement personnel with sufficient time to observe phenological indicators and apply control measures.

Results and Discussion

A) **Woodland Pool** - Larvae of 7 species of mosquitoes were collected in the woodland pool during the springs of 1980, 1981 and 1982 and four species, *Aedes stimulans* (Walker), *Aedes provocans* (Walker), *Aedes euedes* Howard, Dyar and Knab and *Aedes excrucians* were sufficiently common to correlate field development with phenological indicators (Table I). Tables II to V show the dates of development (egg hatch, 80-100 per cent third instar, 100 per cent fourth instar and 100 per cent pupae) for the four previously mentioned species. Table VIII shows the dates for first leaf and bloom of the phenological indicators. Nine indicator plants were reliable to predict the occurrence of 80-100 per cent third instar larvae for one or more of the mosquito species in the woodland pool (Table IX). These plants included Tulip, *Tulipa* spp.; Meadow willow; Clematis, *Clematis verticillaris* DC.; Black current, *Ribes americana* Marsh.; Garden current, *Ribes sativum* Syme; Raspberry; Honey suckle, *Lonicera* spp.; Black cherry, *Prunus serotina* Ehrh.; and Choke cherry, *Prunus virginiana* L.

The first leaf of Raspberry, occurred during the period when larvae of all *Aedes* spp. in the woodland pool were 80 to 100 per cent third instar.

TABLE I. Numbers and per cent species composition of mosquito larvae collected for the woodland, open field and cedar bog pools, Guelph, Ontario, 1980-1982.

	1980 %	1981 %	1982 %
Woodland Pool			
Aedes stimulans	69.2	63.1	80.2
Aedes provocans	2.5	2.8	1.7
Aedes euedes	24.6	32.4	17.3
Aedes excrucians	3.7	1.7	0.8
	N = 4,277	N = 5,358	N = 5,753
Open Field Pool			
Aedes stimulans	18.0	10.0	20.5
Aedes provocans	7.1	7.2	2.3
Aedes euedes	17.6	19.7	29.8
Aedes excrucians	32.3	18.6	11.6
Aedes fitchii	25.0	44.5	35.8
	N = 2,156	N = 1,655	N = 1,089
Cedar Bog			
Aedes stimulans	37.4	32.2	30.6
Aedes provocans	14.5	11.0	39.9
Aedes euedes	1.3	0.8	4.9
Aedes excrucians	35.8	46.5	18.0
Aedes fitchii	3.5	1.0	2.8
Aedes canadensis	7.5	8.5	3.8
	N = 4,224	N = 10,392	N = 642

Several occurrences were common to most of the spring *Aedes* species in the woodland pool. For example the time of egg hatch of *Aedes stimulans*, *Aedes provocans*, *Aedes euedes* and *Aedes excrucians* varied up to 74 days between the springs of 1980 through 1982. Regardless of date of hatch, the appearance of 100 per cent fourth instar larvae for all these species occurred during the first week of May in each year of the study.

B) **Open Field Pool -** Larvae of 7 species of mosquitoes were collected in the open field pool and five species, *Aedes stimulans*, *Aedes provocans*, *Aedes euedes*, *Aedes excrucians*, and *Aedes fitchii* (Felt and Young) were sufficiently numerous to correlate field developmental with phenological indicators (Table I). Tables II through VI show the dates for mosquito development and Table VIII shows the dates for phenological indicators. Ten plants corresponded to the presence of 80 to 100 per cent third instar larvae for one or more of the mosquito species in the open field pool (Table IX). These plants included Tulip; Meadow willow; Squaw current, *Ribes*

TABLE II. Dates of developmental stages for *Aedes stimulans* within the woodland, open field and cedar bog pools, Guelph, Ontario, 1980 - 1982.

	Egg Hatch	80 - 100% instar III	100% instar IV	100% Pupae	Total Days[1]
Woodland					
1980	29 March	22 April	6 May	17 May	50
1981	12 March	10 April	1 May	18 May	68
1982	9 April	26 April	6 May	15 May	37
Open Field					
1980	2 April	20 April	3 May	5 May	34
1981	27 February	9 April	25 April	6 May	69
1982	4 April	23 April	29 April	6 May	33
Cedar Bog					
1980	8 April	9 May	24 May	26 May	49
1981	3 April	24 April	14 May	20 May	48
1982	17 April	7 May	17 May	23 May	37

[1] Days from egg hatch to 100% pupae.

TABLE III. Dates of developmental stages for *Aedes provocans* within the woodland, open field and cedar bog pools, Guelph, Ontario, 1980 - 1982.

	Egg Hatch	80 - 100% instar III	100% instar IV	100% Pupae	Total Days[1]
Woodland					
1980	28 March	19 April	1 May	12 May	46
1981	23 February	7 April	26 April	3 May	70
1982	11 April	26 April	3 May	6 May	26
Open Field					
1980	2 April	19 April	29 April	7 May	36
1981	27 February	1 April	25 April	29 April	62
1982	8 April	20 April	26 April	5 May	28
Cedar Bog					
1980	8 April	25 April	20 May	22 May	45
1981	29 March	7 April	7 May	10 May	43
1982	17 April	28 April	14 May	18 May	32

[1] Days from egg hatch to 100% pupae.

cereum L.; Black current; Garden current; Raspberry; Clematis; Black Cherry; Pin cherry, *Prunus pennsylvanica* L. and Honey suckle.

The first leaf of Raspberry occurred when all species in the open field pool except *Aedes provocans* were 80-100 per cent larvae. As in the woodland pool, despite a wide range of hatching
dates, all species were 100 per cent fourth instar larvae at approximately the same time (last week of April).

C) **Cedar Bog -** Larvae of 7 species of mosquitoes were collected in the cedar bog during the springs of 1980 through 1982 (Table I). These included those found in the open field pool plus *Aedes canadensis*. Tables II through VII show the dates for mosquito development and Table VIII summarizes dates for phenological indicators. Eight plants corresponded to the presence of 80-100 per cent third instar larvae for one or more of the mosquito species in the cedar bog (Table IX). These plants included Tulip; Meadow willow; Yellow birch, *Betula lutea* (Michx. f.); Gray birch, *Betula populifera* Marsh.; Paper birch, *Betula papyrifera* Marsh.; Raspberry; Manitoba maple; and Lilac, *Syringa vulgaris* L.

The first leaf of Lilac occurred when all mosquito species except *Aedes provocans* were 80 to 100 per cent third instar larvae. Larval development between species was less synchronous in the cedar bog, even though egg hatch dates differed by only 29 days during this study.

In grouping the data from all pools, the first leaf of Raspberry and Lilac indicated 80-100 per cent third instar larvae for the most species in the three habitats studied.

TABLE IV. Dates of developmental stages for *Aedes euedes* within the woodland, open field and cedar bog pools, Guelph, Ontario, 1980 - 1982.

	Egg Hatch	80 - 100% instar III	100% instar IV	100% Pupae	Total Days[1]
Woodland					
1980	28 March	22 April	6 May	19 May	53
1981	12 March	10 April	3 May	15 May	65
1982	13 April	26 April	6 May	14 May	32
Open Field					
1980	2 April	24 April	29 April	7 May	36
1981	27 February	7 April	25 April	6 May	69
1982	8 April	23 April	3 May	6 May	29
Cedar Bog					
1980	8 April	9 May	24 May	28 May	51
1981	3 April	24 April	5 May	13 May	41
1982	19 April	7 May	19 May	23 May	35

[1] Days from egg hatch to 100% pupae.

D) **Habitat types** - The development time in the field of the four mosquito species (*Aedes stimulans*, *Aedes provocans*, *Aedes euedes* and *Aedes excrucians*) common to all three pool types was analyzed. The number of days from egg hatch to complete pupation are shown in Tables II to V. In a comparison between pool types using Analysis of Variance, mean development of the mosquito species as a group was significantly ($P<0.05$) faster in the open field and cedar bog pools than the woodland pool. Mosquito larvae required a mean of 49.6 days to reach complete pupation in the woodland pool versus 43.6 and 42.3 days for the open field pool and cedar bog, respectively.

Comparison between species showed that *Aedes provocans* developed significantly ($P<0.05$) faster than both *Aedes stimulans* and *Aedes euedes* in all three pools. The longest period of development (69 days) occurred in the open field pool in 1981 for both *Aedes stimulans* and *Aedes euedes*. *Aedes canadensis* had the shortest development time (24 days), which occurred in the cedar bog in 1982.

The results of this study show that use of plant phenology may have potential to predict larval development of spring *Aedes* mosquitoes. This application would allow mosquito control personnel and homeowners to predict development of larvae in the field by using common plant indicators. More importantly, it would reduce time and resources used to survey early instars. Future research would be useful to test the results reported in this paper in similar habitats across southern and central Ontario.

TABLE V. Dates of developmental stages for *Aedes excrucians* within the woodland, open field and cedar bog pools, Guelph, Ontario, 1980 - 1982.

	Egg Hatch	80 - 100% instar III	100% instar IV	100% Pupae	Total Days[1]
Woodland					
1980	4 April	24 April	8 May	17 May	44
1981	12 March	16 April	6 May	18 May	68
1982	13 April	26 April	3 May	19 May	37
Open Field					
1980	2 April	20 April	29 April	5 May	34
1981	27 February	9 April	30 April	2 May	65
1982	8 April	23 April	3 May	6 May	29
Cedar Bog					
1980	10 April	5 May	24 May	26 May	47
1981	3 April	24 April	14 May	20 May	48
1982	21 April	7 May	14 May	23 May	33

[1] Days from egg hatch to 100% pupae.

TABLE VI. Dates of developmental stages for *Aedes fitchii* within the open field and cedar bog pools, Guelph, Ontario, 1980 - 1982.

	Egg Hatch	80 - 100% instar III	100% instar IV	100% Pupae	Total Days[1]
Open Field					
1980	2 April	24 April	30 April	14 May	43
1981	7 March	11 April	1 May	10 May	65
1982	8 April	23 April	3 May	12 May	35
Cedar Bog					
1980	21 April	5 May	20 May	24 May	34
1981	3 April	24 April	12 May	19 May	47
1982	24 April	7 May	15 May	22 May	29

[1] Days from egg hatch to 100% pupae.

TABLE VII. Dates of developmental stages for *Aedes canadensis* within the cedar bog pool, Guelph, Ontario, 1980 - 1982.

	Egg Hatch	80 - 100% instar III	100% instar IV	100% Pupae	Total Days[1]
Cedar Bog					
1980	16 April	9 May	24 May	30 May	45
1981	6 April	29 April	20 May	24 May	49
1982	26 April	7 May	14 May	19 May	24

[1] Days from egg hatch to 100% pupae.

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TABLE VIII. Mean dates for phenological events for plants located in open, wholly shaded, northern, southern, western, and eastern exposures, Guelph, Ontario, 1980 - 1982.

Plant	Stage	Mean Date 1980	Range	Mean Date 1981	Range	Mean Date 1982	Range
Tulip	1st leaf	23 April	(4)[1]	15 April	(6)	27 April	(4)
	Bloom	29 April	(6)	28 April	(3)	3 May	(4)
Meadow	1st leaf	25 April	(2)	10 April	(3)	27 April	(4)
Willow	Bloom	22 April	(3)	4 April	(4)	19 April	(4)
Birch							
Yellow	1st leaf	5 May	(3)	26 April	(13)	5 May	(3)
Gray	1st leaf	3 May	(3)	28 April	(6)	6 May	(4)
Paper	1st leaf	3 May	(2)	25 April	(8)	5 May	(6)
Clematis	1st leaf	24 April	(3)	12 April	(4)	24 April	(2)
Current							
Squaw	1st leaf	23 April	(3)	5 April	(4)	24 April	(2)
Black	1st leaf	24 April	(2)	5 April	(5)	24 April	(2)
Garden	1st leaf	23 April	(5)	3 April	(4)	23 April	(3)
Raspberry	1st leaf	25 April	(6)	12 April	(5)	25 April	(4)
Cherry							
Pin	1st leaf	29 April	(5)	14 April	(3)	29 April	(5)
Choke	1st leaf	27 April	(3)	14 April	(4)	27 April	(2)
Black	1st leaf	28 April	(7)	14 April	(5)	28 April	(8)
Manitoba Maple	1st leaf	1 May	(6)	8 April	(7)	26 April	(3)
Lilac	1st leaf	5 May	(5)	26 April	(3)	7 May	(8)
Honey Suckle	1st leaf	25 April	(4)	12 April	(2)	26 April	(3)

[1] Number of days over which the various exposures of plants came into 1st leaf or bloom.

TABLE IX. Summary of phenological indicators predicting the period when spring *Aedes* larval populations are 80 - 100 per cent third instar for the woodland, open field and cedar bog pools at Guelph, Ontario, 1980 - 1982.

Plant Species	Woodland Pool	Open Field Pool	Cedar Bog Pool
	Mosquito species 1 2 3 4[1]	Mosquito species 1 2 3 4 5	Mosquito species 1 2 3 4 5 6
Bloom:			
Tulip	- - - -	- - - - -	- - - - 5 -
Meadow Willow	- - - -	- 2 3 - -	- - - - - -
First Leaf:			
Tulip	1 2 - 4	- - - 4 5	- - - - - -
Meadow Willow	1 - 3 -	- - 3 - 5	- 2 - - - -
Yellow Birch	- - - -	- - - - -	- - - 4 5 -
Gray Birch	- - - -	- - - - -	- - - 4 5 -
Paper Birch	- - - -	- - - - -	- - - 4 5 -
Clematis	1 - 3 4	- - - - 5	- - - - - -
Squaw Current	- - - -	1 - 3 4 -	- - - - - -
Black Current	1 - 3 -	- - 3 - 5	- - - - - -
Garden Current	- 2 - -	- 2 3 - -	- - - - - -
Raspberry	1 2 3 4	1 - 3 4 5	- 2 - - - -
Pin Cherry	- - - -	- - - 4 5	- - - - - -
Choke Cherry	- - - 4	- - - - -	- - - - - -
Black Cherry	1 - 3 4	- - - - 5	- - - - - -
Manitoba Maple	- - - -	- - - - -	- 2 - - - -
Lilac	- - - -	- - - - -	1 - 3 4 5 6
Honey Suckle	1 - 3 -	- - - - 5	- - - - - -

[1] Mosquito species: 1 = *Aedes stimulans*
2 = *Aedes provocans*
3 = *Aedes euedes*
4 = *Aedes excrucians*
5 = *Aedes fitchii*
6 = *Aedes canadensis*

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THE LIFE CYCLE OF *SERRATELLA DEFICIENS* (MORGAN) (EPHEMEROPTERA: EPHEMERELLIDAE) IN OAKVILLE CREEK, SOUTHERN ONTARIO

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Serratella deficiens (Morgan) has a univoltine cycle in southern Ontario. The emergence of adults extends from late May to late July. The eggs hatch within a few weeks, and the nymphs grow rapidly until November. There is no further development in winter. Growth resumes in late April and is completed within the next one to three months. Male and female nymphs show little difference in their growth patterns. There is a wide range of sizes in the nymphal population throughout the year, especially during the last months of the cycle. The late emergence of the species, relative to other Ephemerellids, does not seem to allow the resynchronisation of the cycle commonly observed in spring species.

Introduction

Serratella deficiens (Morgan) is a common inhabitant of riffle areas (Sweeney and Vannote 1981) in medium to large streams throughout the northeastern Nearctic region (Allen and Edmunds 1963). In Eastern Canada, it occurs both in the hard-water streams of the St. Lawrence lowlands and in the soft-water streams of the Canadian Shield. Its life cycle has been described by Sweeney and Vannote (1981) in Pennsylvania, by Coleman and Hynes (1970) in the Speed River in southern Ontario, and by Peterson and Martin-Robichaud (1986) in New Brunswick. These studies indicate a univoltine cycle with the species overwintering as a nymph. Sweeney and Vannote (1981) show the nymphs to be present in the stream from September to late-May when the species emerges, and indicate a short incubation period for the eggs (36 - 41 days), but Coleman and Hynes (1970) suggest the probability a long egg diapause lasting from June until December. Peterson and Martin-Robichaud's (1986) account, while somewhat sketchy, agrees more with that of Sweeney and Vannote (1981).

While sorting out material collected in southern Ontario during an earlier study on the ecology of Plecoptera (Harper and Hynes 1972; Harper 1973), we came across a series of nymphs of *S. deficiens* from Oakville Creek. This series illustrates, much better than previous accounts, the life cycle of the species, and therefore seems to be well worth recording.

Methods

Ten samples of benthos were collected at regular intervals between July 8, 1969 and May 30, 1970, following the "kick-sampling" method of Hynes (1961). In order to counter the selectivity

of one mesh opening, two hand nets were used, of respective mesh-sizes of 900 and 60 microns. Both samples were pooled, fixed in formalin, stored in alcohol, and later elutriated in a saturated solution of $CaCl_2$; the nymphs were then handpicked under a stereo-microscope (6-12X). Subsampling with a Folsom-type plankton partitioner was necessary when material was too abundant (McEwen *et al.* 1954).

Nymphs were measured (from clypeus to apex of 10th abdominal segment) and grouped into classes of 0.25 mm. Given the large number of nymphs (N = 5,125), total length was felt to be an adequate measure of growth, rather than the less variable head width. The size-frequency diagram (Fig. 1) illustrates the life cycle. Sexes could be determined in larger nymphs and, just before emergence, also in mid-size individuals.

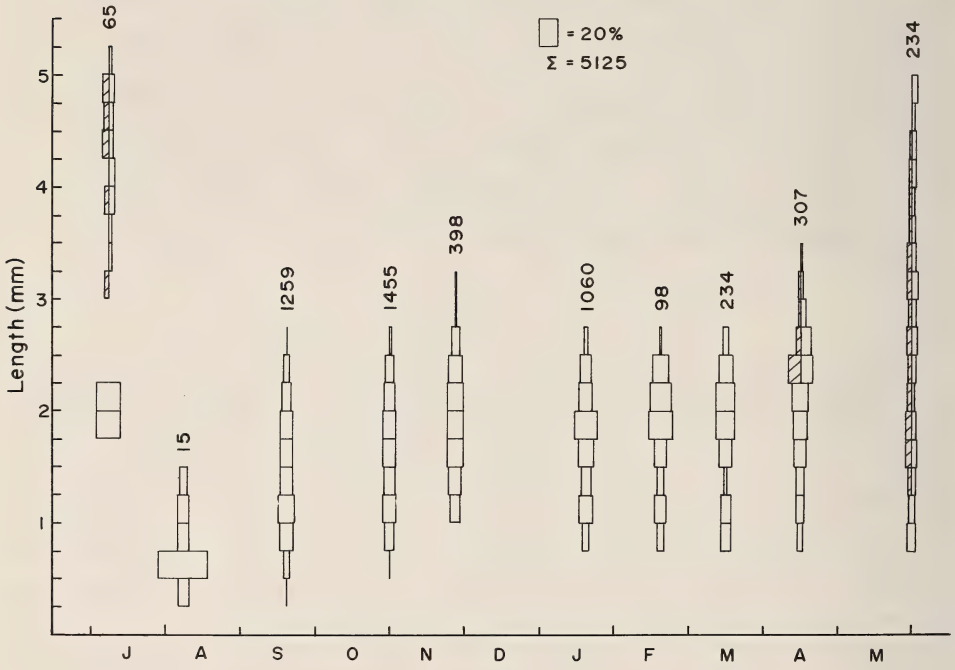

FIGURE 1. Life cycle of *Serratella deficiens* in Oakville Creek, southern Ontario: size-frequency distribution of the body lengths of the nymphs over a 12 month period. The cross-hatched diagrams represent the male nymphs. Numbers over each diagram indicate the size of the sample.

Study site

Oakville Creek flows west over the Niagara Escarpment into Lake Ontario. The sampling station was just upstream from the town of Campbellville (79° 56' W, 43° 29' N) in Halton County. The stream is large (5-6 m wide and 0.3-1.0 m deep) and the substrate consists of cobbles and gravel. The drainage area is mostly deforested and largely agricultural, which accounts for

wide variations in the flow. The water chemistry was typical of the hard-water streams of the area: pH = 7.9, conductivity 485-500 µS, hardness 230-290 mg $CaCO_3$ (Harper and Hynes 1972). Summer water temperatures (May - August) ranged from 20 to 23°C, and winter water temperatures (December - April) remained close to 0°C. Despite the freezing temperatures, the riffles did not freeze over. However, there was extensive icing near the shores. Anchor and frazil ice frequently developed on the bottom.

The mayfly community was rich and represented by seven families; these are listed here by order of decreasing importance (% of the 26,104 nymphs collected): (1) Leptophlebiidae 39.3% (*Paraleptophlebia* spp. 39.1%); (2) Ephemerellidae 24.6% (*S. deficiens* 19.6%, *Ephemerella subvaria* McDunnough 3.1%, *E. dorothea* Needham, *E. needhami* McDunnough, *E. rotunda* Morgan, and *Eurylophella bicolor* Clemens); (3) Baetidae 23.0%; (4) Isonychiidae 5.3% (*Isonychia bicolor* (Walker)); (5) Heptageniidae 5.1% (*Stenonema* spp. 3.7%, *Epeorus* spp.); (6) Caenidae 2.7% (*Caenis* spp.); (7) Ephemeridae 0.02% (*Ephemera* spp.).

Results

The nymphs of *S. deficiens* were present in the stream throughout the year (Fig. 1). The mature nymphs occurred from late May to mid-July, which indicates an extended emergence of the adults of approximately two months. By early August, the new cohort of nymphs had appeared and some of the nymphs had already undergone considerable growth, measuring up to 1.5 mm, from 0.5 mm at hatching ($\bar{x}$ = 0.87 ± 0.28 mm). Growth continued into November (September $\bar{x}$ = 1.56 ± 0.47 mm; October $\bar{x}$ = 1.78 ± 0.50 mm; November $\bar{x}$ = 2.00 ± 0.45 mm), after which no change in the population was observed until April (January $\bar{x}$ = 1.84 ± 0.45 mm; February $\bar{x}$ = 1.97 ± 0.44 mm; March $\bar{x}$ = 1.94 ± 0.5 mm). Growth then resumed and was completed within one to three months (April $\bar{x}$ = 2.28 ± 0.53 mm; May 1970 $\bar{x}$ = 3.31 ± 1.00 mm; May 1969 $\bar{x}$ = 3.32 ± 1.20 mm). The nymphs overwintered at sizes ranging from 0.75 to 2.5 mm, at approximately mid-growth, since the mature nymphs measured 4.25 to 5.25 mm at least at the beginning of the emergence period; late emergers, recognized by the presence of full-grown wing-pads, were slightly smaller. The size range of nymphs, already wide in winter, increased considerably in the spring, as nymphs varying from 0.75 to 5.0 mm were encountered in May.

There was little difference between the growth of male and female nymphs, and both sexes seemed to mature at the same time and reached comparable final sizes.

Discussion

This detailed account of the nymphal growth of *S. deficiens* confirms the earlier report by Sweeney and Vannote (1981) of a univoltine cycle, with a short incubation period of the eggs, nymphal growth taking place in late-summer and autumn and resuming in late-spring and early-summer, and no significant development during the winter months. It does not support Coleman and Hynes' (1970) suggestion that "this species may have a long egg-diapause and hatch and grow only during the coldest season", although their diagram indicates no growth after February. Overwintering occurs at an average total length of 2 mm both in our and Coleman and Hynes' (1970) data.

The emergence pattern in southern Ontario is probably of the type illustrated by Sweeney and Vannote (1981, Fig. 2), consisting of a fortnight of heavy emergence, followed by some three weeks at a much decreased rate.

The wide range of sizes in the nymphal population at any one season had not been described previously, and it probably results from the relatively long emergence period of the adults. Although the eggs hatched rapidly, they were laid over a period of nearly two months and hatchlings were present in the stream until mid-September. This does not explain, however, the great increase in the range of nymph sizes observed in May. No doubt, some of the nymphs were able to grow much more rapidly than others and emerge early, while others seemed to straggle on at a much slower pace. In July, some of these smaller nymphs (1.75 to 2.25 mm) appeared to have been left behind; they were no longer there in August and had either died off or else emerged late at a smaller size.

Being one of the later emerging species, *S. deficiens* completes a greater percentage of its growth in the spring than other syntopic species (e.g. *E. invaria*, *E. subvaria*, *E. dorothea*, *Eurylophella* spp.); it is also much less synchronised in its nymphal growth. Whether this lack of synchrony is due to the late emergence in summer, or is related to competition among the co-existing Ephemerellids, which all share a common food source (they feed equally on diatoms and detritus in the riffle areas (Sweeney and Vannote 1981), a diet not particularly different from other stream Ephemerellids (Hawkins 1986)) is unclear; the first hypothesis, however, appears more likely. The phenomenon could be due to differential growth rates in nymphs of various sizes resulting in a decrease in synchrony rather than the usual increase generally observed in spring species. By the time this species approaches maturity in June and July, stream temperatures have reached their summer plateau. Therefore no re-synchronisation mechanism, such as postulated by Sweeney and Vannote (1981), which is dependent on increasing stream temperatures, is available. No re-synchronisation can therefore occur, hence the rather extended emergence, characteristic of this, and many other, "summer species" (Harper and Magnin 1971).

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PEAR THRIPS, *TAENIOTHRIPS INCONSEQUENS* (UZEL) (THYSANOPTERA: THRIPIDAE), ON SUGAR MAPLE IN ONTARIO

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Pear thrips (*Taeniothrips inconsequens* [Uzel]) has recently become a major concern to foresters in the northeastern United States and Canada. A review of its history, hosts and damage and a description of its life history is presented.

The results of Ontario surveys conducted by the Forest Insect and Disease Survey Unit in 1989, 1990, and 1993 are presented. The insect is present throughout the range of sugar maple (*Acer saccharum* Marsh.) in Ontario. Other trees upon which it was found include basswood (*Tilia* spp.), jack pine (*Pinus banksiana* Lamb.) and black ash (*Fraxinus nigra* Marsh.).

Introduction

Pear thrips (*Taeniothrips inconsequens* [Uzel]) has recently become a major concern to foresters in the northeastern United States, especially in Pennsylvania, New York, New Hampshire, Massachusetts, Maine, Connecticut and Vermont. The insect has caused widespread damage to sugar maple (*Acer saccharum* Marsh.) during the mid-to-late 1980s (Parker *et al.* 1988). When forest managers realized the observed damage to sugar maple and other forest species was caused by this insect, studies on its biology, life history, detection and control were initiated throughout the northeastern states by several state, federal and university groups (Parker *et al.* 1988, 1990, 1991; Parker and Doane 1991).

Foresters and sugar-bush owners throughout this region and beyond, to the bordering provinces of Quebec and Ontario, were concerned for the future of their trees. Quebec forestry officials were aware of the insect's presence at the time, but damage had not been observed. Its occurrence in Ontario forests was unknown (Parker *et al.* 1988). The Forest Insect and Disease Survey (FIDS) Unit of Natural Resources Canada, Canadian Forest Service, Ontario Region, initiated a survey to determine pear thrips distribution within the range of sugar maple. The results are reported here.

History

Bailey (1944) reported that the first published record of pear thrips was its original description from Bohemia (The Czech Republic) in 1895 by Uzel. However, Williams (1913, 1916) argued for its existence in England in 1829. Parrot (1912), Foster and Jones (1915), Cameron and Treherne (1918), and Bailey (1944), reported its discovery and occurrence throughout England, Europe and North America. The insect's world distribution includes France, Italy, Denmark,

Germany, The Czech Republic, Austria, Finland, Norway, Sweden, Crimea, Turkestan (former U.S.S.R.), England, Scotland, Central Asia, Cyprus, and Japan. It is also found in South America, from Argentina and Brazil. Early records associated it with economic damage, primarily to pear (*Pyrus* spp.) and prune (*Prunus* spp.) orchards but other orchard crops were also affected (Foster and Jones 1915; Cameron and Treherne 1918).

During 1904, in California, this insect caused the first serious economic damage to pears in North America (Daniel 1904; Bailey 1944). Foster and Jones (1915) suggested, however, that unrecognized, it first attracted attention in that state in 1902. Parrot (1912) documented its early spread throughout the northeastern United States.

In 1915, pear thrips was first discovered infesting orchards near Royal Oak on Vancouver Island, Canada (Cameron *et al.* 1916). At that time it had not been detected on the adjacent mainland of British Columbia. Although not previously observed, Cameron and Treherne (1918) felt the insect had been on the island for some 10 or more years.

In May 1969, pear thrips was recorded infesting an apple orchard near the Vermont border in southwestern Quebec (Paradis 1969; Hébert 1992). Coli (1990) reported, in 1988, the absence of pear thrips on maple in southern Quebec. Bonneau (1990), however, reported that pear thrips on sugar maple was found readily in the St. Lawrence Plain of Quebec in 1989. Damage was considered small. Surveys done in 1989 and 1990 by the Service de la Protection contre les Insectes et les Maladies of the Ministère des Forêts du Québec showed that pear thrips was distributed throughout the forest stands of the province. This suggests the insect has been in Quebec for a long time (Hébert 1992).

A record of pear thrips, in fruit orchards in the Annapolis Valley of Nova Scotia in 1932, may be that province's first record (Gilliatt 1932). New Brunswick monitored maples for pear thrips for the first time in 1989 and found the insect at five locations (Dearborn 1990; Moody 1992, 1993). The examination of sugar maple for the presence of pear thrips was undertaken in 1990 by the Maritime provinces. Although damage was negligible, it was found in Nova Scotia, New Brunswick and Prince Edward Island (Moody 1993).

The first record of pear thrips in Ontario was in a pear orchard near Beamsville in 1918 (Ross and Caesar 1919). Populations were small and damage was rare. Ross and Caesar (1919) suggested that pear thrips had been present in orchards in the Niagara district for several years but the insect had gone unnoticed because of low numbers. Recent observations by the Ontario Ministry of Agriculture and Food (OMAF) confirm that it has never been a serious pest of fruit trees in the province (K. Kerr, OMAF, Vineland Station, Ont., pers. comm.).

The Forest Insect and Disease Survey (FIDS) Unit in Ontario has not recorded this insect within forest stands since records began in 1946. However, because pear thrips have cryptic habits, it would have been overlooked unless damage was evident or it had been collected incidentally.

Hosts

Pear thrips derives its common name from its early occurrences on pear trees. It has long been associated, however, with other hosts in the family Rosaceae, and with many non-fruit trees (Foster and Jones 1915; Cameron and Treherne 1918; Bailey 1944). Some hosts on which it reproduces (Bailey 1944) include species as disparate as broadleaved evergreens, wild cherry (*Prunus* spp.), willow (*Salix* spp.) and poison oak (*Rhus* spp.). Non-hosts (i.e., those on which development has not been confirmed, but on which the insect has been found) include a variety

of trees, shrubs and herbs, e.g., grasses, skunk cabbage (*Symplocarpus foetidus* [L.] Nutt.) and dandelion (*Taraxacum* sp.) (Foster and Jones 1915; Cameron and Treherne 1918; Bailey 1944). Maple is included in the list of tree hosts (Cameron and Treherne 1918; Bailey 1944). Cameron and Treherne (1918) showed that the insect reproduced on bigleaf maple (*Acer macrophyllum* Pursh) in British Columbia. The recent concern in the American Northeast (Parker *et al.* 1988, 1990) has been elicited by the severity of attack by pear thrips primarily on sugar maple.

Description of Pear Thrips Damage

Foster and Jones (1915), Lewis (1973) and Chisholm and Lewis (1984) describe the structure and action of the mouthparts of plant-feeding thrips in detail. Pear thrips feed by penetrating a plant's epidermis with mouthparts that are specially modified for this purpose. The walls of adjacent cells below the leaf's surface are broken down, and the plant juices that ooze from the ruptured cells are taken up. Detailed descriptions of specific damage to pear crops, other fruit crops and other trees are given by Foster and Jones (1915), Cameron and Treherne (1918) and Bailey (1944).

Pear thrips causes damage during three major parts of its life cycle: adult feeding, oviposition and larval feeding. Damage to sugar maple is caused initially by the adult thrips feeding within the expanding blossom buds and vegetative buds. As the buds begin to expand, brown margins show on the newly expanding leaves. This damage superficially resembles frost damage. Furthermore, necrotic tissue forms around feeding wounds and the expanding leaves become distorted, dwarfed, and "shot-holed" as nonexpandable necrotic tissue falls out of the leaf during growth. Leaves may prematurely drop to the ground. Later, as the leaves expand, female thrips, using the toothed ovipositor, insert eggs into the leaf tissue (Cameron and Treherne 1918; Bailey 1944), usually along main veins on the undersides of leaves or along the leaf petioles. A brown scar forms around oviposition sites resulting in further leaf distortion. Larval feeding is similar to that of the adult, causing further damage to the leaf blade. Expanded leaves appear mottled and puckered, may have a ragged or torn appearance, and the crown appears thinly foliated. Pear thrips damage reduces a tree's vigour, stunts growth, and increases susceptibility of attacks by other organisms (Parker *et al.* 1988).

Description of Pear Thrips

Pear thrips eggs are whitish, colourless, and bean-shaped. They measure 0.75 mm long by 0.25 mm wide (Cameron and Treherne 1918).

The larval stage has two instars. Upon hatching, the larva or nymph is translucent white with bright red eyes. The antennae are 7-segmented (Nakahara 1991). After moulting once, the second-stage larva is slightly larger and yellowish white in colour. According to Nakahara (1991), the larva is characterized by a distinctive row of large, sclerotized, dorso-lateral teeth found on the posterior margin of abdominal segment nine. These teeth are more noticeable in the second instar (Nakahara 1991; Skinner *et al.* 1991).

The prepupa and pupa are similar to the adult. The wing-pads are beginning to develop in the prepupa but lack fringes in both stages. Antennae of the pupa are folded back over the head. When the wing-pads reach beyond the base of the abdomen, it is considered a pupa (Skinner *et al.* 1991).

The adult is brown to black (Skinner *et al.* 1991), slender and about 1.5 mm long. The head is wider behind prominent black eyes with light borders (Foster and Jones 1915), and the ocelli are yellow to reddish brown in colour. Antennae are 8-segmented, and the apical part of segment II and basal part of segment III are lighter in colour (Nakahara 1991). Legs are generally brown except the tarsi and bases of tibiae and femora are yellow (Foster and Jones 1915; Nakahara 1991). According to Nakahara (1991), the apical claws on the foretarsi are distinctive. Wings are long, narrow and fringed with long hairs.

Life History of Pear Thrips

The life history of pear thrips on sugar maple in Ontario is not known, but, its life history in western pear orchards has been described (Foster and Jones 1915; Cameron and Treherne 1918; Bailey 1944). Sarazin *et al.* (1990) gave a brief synopsis of the insect's life history, description and damage potential.

Coincident with the expansion of the maple buds, the adult emerges in the spring from an earthen cell made by the larva in the previous season. The female flies to a host tree, crawls in under or between the bud scales and begins feeding.

When the buds open, eggs are laid along the petioles and main veins by inserting the toothed ovipositor into the tissue. With magnification, the eggs show as raised areas on the veins. The duration of the egg stage, which is dependent on the weather and other factors, is approximately ten days (Foster *et al.* 1915; Cameron *et al.*, 1918). After two or three weeks of feeding, the larva drops to the ground and enters the soil. Construction of a cell occurs within the mineral soil at depths down to 40 cm (Cameron and Treherne 1918; Sarazin *et al.* 1990). Although only one larva exists per cell, the cells are often grouped. The larvae remain dormant in the soil until the fall (Cameron *et al.* 1918; Skinner *et al.* 1991) when the prepupal stage forms. After seven to ten days, the prepupa transforms into the pupal stage which lasts between six weeks and two months (Cameron *et al.* 1918). The adult overwinters in the soil cell and emerges in the spring when soil temperature or moisture conditions are right. Females bear about 200 eggs. Males are unknown in North America, although both sexes occur in Europe (Stannard 1968).

The Ontario Survey

Method

The FIDS Unit undertook a major detection survey for pear thrips throughout the range of sugar maple in Ontario in 1989, 1990 and 1993. Time restraints prevented conducting a quantitative survey.

For the year 1989, each ranger sampled ten sugar maple locations if the tree species was present within his work area. Between May 1 and May 24, a total of 93 locations was sampled for larvae and/or adults. South-facing or ridge-type sites were selected since damage is most noticeable on south or west-facing slopes and at higher elevations (Bailey 1944; Rock and Vogelmann 1988). Ten flower clusters were sampled using pole pruners. Samples were taken from each of three open-grown trees or trees on the edge of stands from as high as practicable. The mean tree height was 18.8 m ± 4.9 m, ranging from 10 m to 40 m. If flower clusters could not be found, then an early terminal leaf cluster was collected. The flower or terminal leaf cluster

from each site was placed in a 230-ml jar containing a 75% ethanol solution and examined at Natural Resources Canada's Sault Ste. Marie laboratory. Damage by pear thrips was noticeable in August and a further nine locations were examined. Two of these nine locations had previously been examined for the presence of larvae and/or adult thrips.

In 1990, collections were made in localities where pear thrips had not been sampled or found in 1989. A total of 32 collections was made during that year from May 8 to May 23. The mean tree height was 18.8 m ± 4.9 m, ranging from 10 m to 40 m. During August, damage by pear thrips was observed in two localities not previously surveyed.

In 1993, Dr. R. Footit from the Biosystematics Research Division (BRD), Agriculture Canada, requested assistance from FIDS to collect pear thrips on sugar maple for a study on climate matching techniques. A total of 48 locations was sampled. Dr. Footit received flower clusters and/or expanding leaves from May 11 to May 17. The mean tree height of the locations examined was 16 m ± 3.5 m. The height of the trees ranged from 10 m to 25 m. Damage by pear thrips was not observed later in the season.

The Biosystematics Research Division, Ottawa identified all thrips. Natural Resources Canada's Sault Ste. Marie laboratory examined damaged leaves.

Results

Distribution

Pear thrips was collected in 1989 from the Sault Ste. Marie, Sudbury, North Bay, Algonquin Park, Pembroke, and Bancroft districts of the Ontario Ministry of Natural Resources (OMNR) Central Region, and from Kemptville, Tweed, Maple, Midhurst, and Cambridge districts of the Southern Region (Fig. 1).

In the summer of 1990, pear thrips was found at new locations in the Sault Ste. Marie, Sudbury, and Parry Sound districts of the Central Region, and from Tweed, Midhurst and Aylmer districts of the Southern Region (Fig. 2).

In 1993, pear thrips was collected from the Sault Ste. Marie, Sudbury, North Bay and Parry Sound districts of the Central Region, and from Kemptville, Tweed, Midhurst and Aylmer districts of the Southern Region (Fig. 3). Specific locations of pear thrips collections are on file and are available from the authors.

Damage

Pear thrips was found, in low numbers, throughout the range of sugar maple in Ontario. During the 1989 survey, 61% of all the locations sampled were found to have pear thrips. The mean number of pear thrips found per sample at positive locations was 18.8 ± 27.8 ranging from 1 to 176. At a few locations where pear thrips adults and/or larvae had been collected, some foliar damage was noted later in the season. Light damage was recorded at locations in Tweed, Maple, Cambridge and Midhurst districts (Fig. 1).

During 1990, 50% of all locations sampled were found to have pear thrips. The mean number of pear thrips collected per sample at positive locations was 18.8 ± 5.0 with a range from 1 to 21. Low damage levels were reported on understory sugar maple from one site each in Ross township, Pembroke District and Oakville, Maple District. Damage was more prevalent on open grown sugar

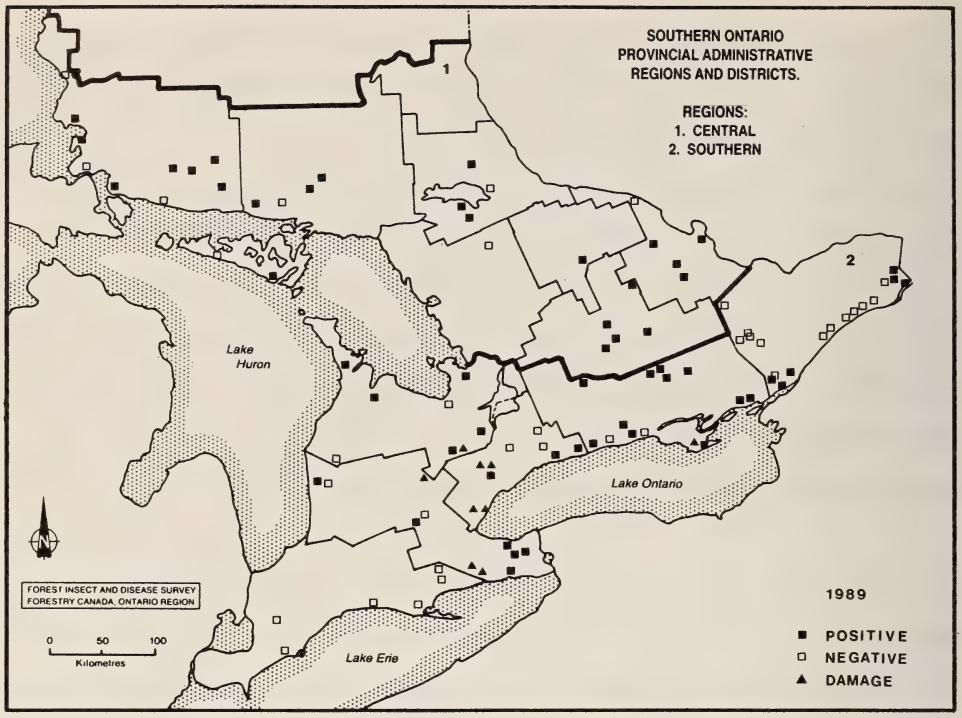

FIGURE 1. Survey of pear thrips on sugar maple in Ontario, 1989.

maple. During 1989 and 1990, when damaged leaves were examined microscopically, pear thrips oviposition scars along the main vein and petiole were seen.

Pear thrips was present in 42% of the locations sampled in 1993. The mean number of pear thrips collected per sample at positive locations was 9.3 ± 19.0, ranging from 1 to 85. During this year, no noticeable damage was reported.

Other Thysanoptera Collected

Other species of Thysanoptera found on sugar maple, during the same surveys, include basswood thrips (*Thrips calcaratus* Uzel), flower thrips (*Frankliniella tritici* [Fitch]), black hunter thrips (*Leptothrips mali* [Fitch]), and *Haplothrips* spp.

Non Hosts

During the summer of 1989, pear thrips was collected by FIDS rangers on basswood (*Tilia* spp.) in Thorah Township, Maple District, and at two locations in North Burgess Township, Kemptville District in the Southern Region; on jack pine (*Pinus banksiana* Lamb.) in Montague Township, Kemptville District in the Southern Region; and on black ash (*Fraxinus nigra* Marsh.)

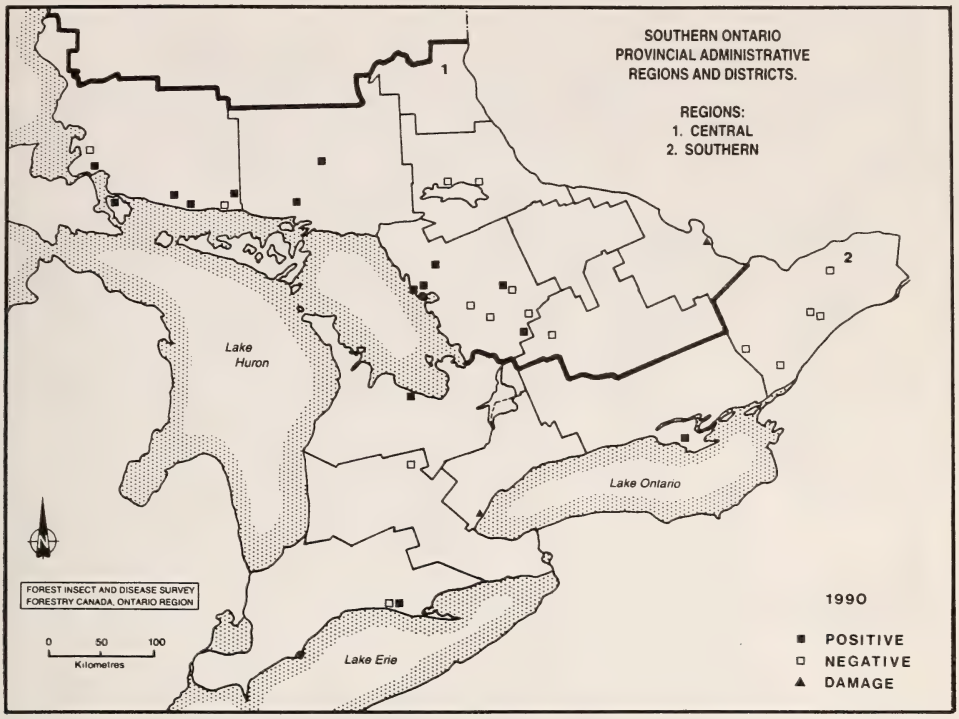

FIGURE 2. Survey of pear thrips on sugar maple in Ontario, 1990.

in Sadler Township, Chapleau District in the Northeastern Region. For this survey, it was not learned whether pear thrips could reproduce on these tree species. All thrips specimens were confirmed at BRD in Ottawa.

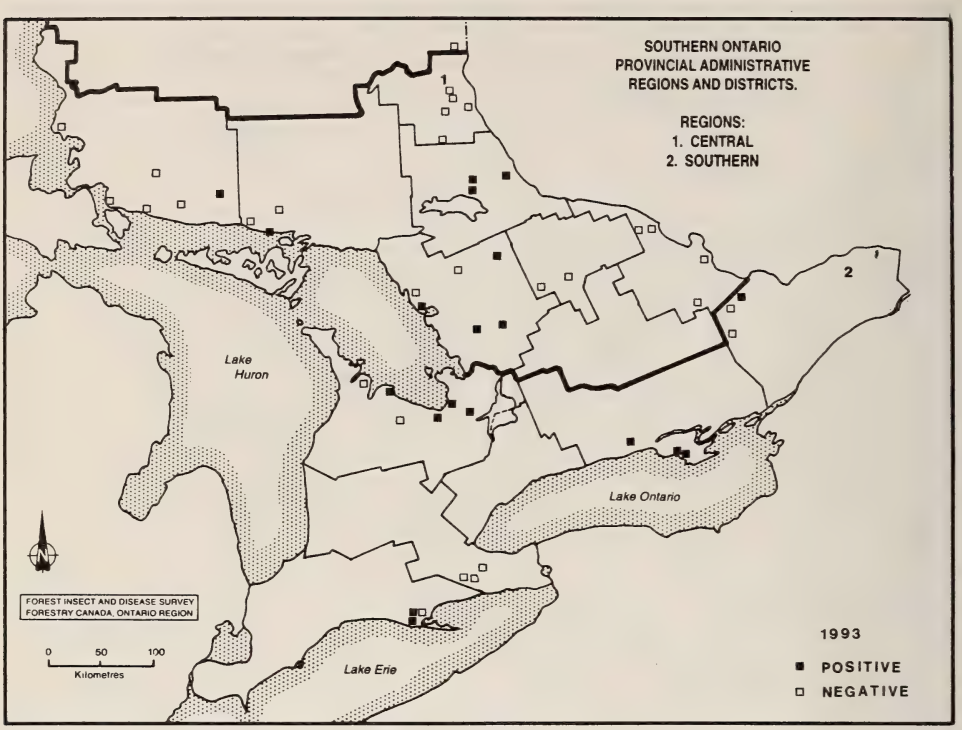

FIGURE 3. Survey of pear thrips on sugar maple in Ontario, 1993.

Acknowledgments

We thank the rangers of Natural Resources Canada, Canadian Forest Service, Ontario Region's Forest Insect and Disease Survey Unit for their assistance in collecting the samples. We also thank Dr. R. Foottit and Mr. M. Maw, BRD, Ottawa, for identification of thrips species.

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RESPONSES TO FIRE BY TAIGA SPIDERS

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Abstract *Proc. ent. Soc. Ont.* 125: 29-41

The basic objective of this study was to determine those possible pioneer and climax species from disturbed and undisturbed plots respectively. In southeastern Manitoba, pitfall transects in freshly-burnt and control bogs, dominated by *Picea mariana*, and pine ridges, dominated by *Pinus banksiana*, collected a total of 69 species of spiders, with 50 species taken from burned plots and 45 from control plots; 26 species were common to both plots. Species preferring burned plots included four species of *Pardosa*, *Alopecosa aculeata* (Clerck), *Trochosa terricola* Thorell (all in the family Lycosidae), *Agroeca ornata* Banks (Liocranidae), *Erigone atra* Blackwall (Erigonidae), *Pocadicnemis americana* Millidge (Erigonidae), *Tunagyna debilis* (Banks) (Erigonidae), and *Bathyphantes pallidus* (Banks) (Linyphiidae). Species found only in control plots included *Hogna frondicola* (Emerton (Lycosidae), *Gnaphosa microps* Holm (Gnaphosidae) and *Neoantistea agilis* (Keyserling) (Hahniidae). Numbers were high for two months after the fire and then decreased, following usual seasonality and activity patterns.

Résumé *Proc. ent. Soc. Ont.* 125: XX-XX

L'objectif de cette étude était de déterminer les espèces possiblement de pionnier et de climax prises dans des endroits bouleversés et des endroits non bouleversés réspectivement. Dans le sudest du Manitoba des transects de trappes du fond, placés dans les tourbières, dominées par *Picea mariana*, et des arêtes du pin, dominées par *Pinus banksiana*, récement brulées et des controlles, ont ramassés 69 espèces d'araignées, avec 50 espèces prises des endroits de controlle, et 26 espèces communes entre les deux. Des espèces, préfèrant les endroits brulés, comprennaient quatre espèces de *Pardosa*, *Alopecosa aculeata* (Clerck), *Trochosa terricola* Thorell (toutes dan la famille Lycosidae), *Agroeca ornata* Banks (Liocranidae), *Erigone atra* Blackwall (Erigonidae), *Pocadicnemis americana* Millidge (Erigonidae), *Tunagyna debilis* (Banks) (Erigonidae), et *Bathyphantes pallidus* (Banks) (Linyphiidae), pendant que les espèces évitant des endroits brulés comprennaient *Hogna frondicola* (Emerton (Lycosidae), *Gnaphosa microps* Holm (Gnaphosidae) et *Neoantistea agilis* (Keyserling) (Hahniidae). Les nombres étaient élèvés pendant les premiers deux mois aprés le feu et ensuite étaient diminués, suivant la saisonalité habituelle et les modeles d'activités.

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Keywords: post-fire, succession, spiders, Araneae, arachnids, Manitoba, burns, taiga, boreal forest, disturbances

Introduction

In the province of Manitoba taiga extends from 49° to 60°N. The taiga typically composed of a black spruce (*Picea mariana* (Mill.) B.S.P.) community (Shay 1984), is characterised by periodic fires which kill overstory trees and most vegetation above ground (Kelsall *et al.* 1977; Larsen 1980; Viereck 1983). In its southern reaches birch (*Betula* spp.) and aspen (*Populus* spp.) commonly invade black spruce (Viereck 1983) and provide excellent fuel for ground fires (Kelsall *et al.* 1977; Larsen 1980). The relative intensity of a burn is dependent upon the moisture content of vegetation and litter, slope, wind turbulence and density of tree cover (Bunting 1983; Furayaev and Zlobina 1985). The rate of vegetative recolonisation is slow after an intense burn (with aspen an exception), and more rapid after a partial burn, with mosses and vascular plants first to invade (Larsen 1980; Bunting 1983).

Faunal succession follows that of the vegetation, be they insects (Danks and Foottit 1989), spiders (Huhta 1971; Riechert and Reeder 1972; Schaefer 1980; Weaver 1985; Koponen 1989), or small mammals and birds (Fox 1983). In the case of carabid beetles, the microclimate provided by the vegetation is probably most important for their distribution (Richardson and Holliday 1982), and this may well also be the case for spiders.

Most studies involving post-fire recolonisation by insects and spiders have taken place in habitats other than the taiga, such as in pine forests of southern Germany (Schaefer 1980; Winter 1978, 1980; Winter *et al.* 1976, 1983), mostly pine forest of maritime Scandinavia (Huhta 1971; Solbraa 1979; Hauge and Kvamme 1983), and old fields and prairies of the central United States (Riechert and Reeder 1972; Bultman and Uetz 1982; Weaver 1985; Haskins and Shaddy 1986). Only in northern Finland have Huhta (1971) and Koponen (1988, 1989) followed post-fire recolonisation of spiders in a taiga habitat, as well as recolonisation of clear-cut areas in pine and spruce stands and in birch forests.

The objectives in this study were to determine: 1) those species which are pioneer species in the burnt plots; 2) those species found only in control plots; 3) those species common to both burns and control plots; and 4) preferences of various species for burns and control plots.

The spiders are grouped in guilds, defined by Bultman and Uetz (1982) as ecological groups of organisms which exploit a single or similar resource in a like manner. They consist of an erigonid-linyphiid guild and a cursorial guild, subdivided into a lycosid guild and a guild of other cursorial spiders (families Gnaphosidae, Clubionidae, Agelenidae, Hahniidae, Thomisidae, Philodromidae, Salticidae and Dictynidae). The relatively large number of spiders, the ease of collection and the relative ease of identification (Schaefer 1980) make these invertebrates suitable organisms with which to work.

Locality, Materials and Methods

The study site is located close to the Taiga Biological Station (51°02'N, 95°20'W) north of Wallace Lake in southeastern Manitoba, where a fire swept through the area on 6 May 1987. Six different plots were selected: 1) an intensely burnt black spruce bog (I), burnt in 1987 10 cm into the peat with bare black *Sphagnum* peat and charred spruce trunks (*P. mariana*) (later in the season

TABLE I. The number of spider species from Erigonidae-Linyphiidae (Erig-Lin), Lycosidae (Lyc) and other cursorial species (Curs) guilds from burns and control plots, with the number in brackets representing species common to both plots.

	Erig-Lin	Lyc	Curs
Burns	23 (6)	10 (9)	17 (11)
Controls	16	10	19

some herbaceous growth occurred); 2) a less intensely burnt black spruce bog (L), burnt 0-6 cm into the peat in a sporadic manner in 1987, leaving some charred trunks of *P. mariana* and *Larix laricina* (DuRoi) K. Koch, some living of the same, burnt and living *Ledum groenlandicum* Oeder, *Salix* spp., *Vaccinium* spp., and *Sphagnum* spp.; 3) a black spruce bog burnt in the summer of 1980, the only available area closest to a "control" bog (B), with deadfall of *P. mariana*, some *L. groenlandicum*, *Smilacina trifolia* (L.) Desf. and *Sphagnum* spp.; 4) a fresh burn (F) on a jack pine ridge (*Pinus banksiana* Lamb.) burnt 10 cm into the humic matter in 1987, with bare rocks, charred soil, peat and tree trunks; 5) an intermediary plot of an old burn (1980) on a jack pine ridge (O), with much deadfall of *P. banksiana*, *P. mariana*, *Populus tremuloides* Michx., regrowth of *Salix* spp. up to 2 m, "fire moss" *Ceratadon purpureus* (Hedw.) Brid., *Aralia hispida* Vent. and *Epilobium angustifolium* L.; and 6) an undisturbed jack pine ridge (R) at Raven's Cliff with climax vegetation of *P. banksiana*, *Betula papyrifera* Marsh., *Salix* spp., *Amelanchier alnifolia* Nutt., *Vaccinium* spp., *Juniperus horizontalis* Moench., *Arctostaphylus uva-ursi* (L.) Spreng., lichens and feather mosses, approximately 100 years old (Martin 1983; Schaefer and Pruitt 1991).

A transect of 6 pitfall traps of polystyrene plastic with lips set at ground level (6 m apart, 6.5 cm diameter), was placed in each plot of about 0.5 ha. Continuous sampling was done from 6 June 1987 to 4 October 1987, emptying traps about every three weeks. Traps contained a mixture of 50% ethylene glycol and 50% water to preserve the catch; they were protected from exposure by a curved piece of asphalt shingle (about 20 cm x 40 cm). The distance between plots and the difficulty in reaching them, especially in autumn, prohibited extensive trapping in any area.

In the laboratory, specimens were rinsed in water, placed in 70% ethanol, sorted, identified and counted. The preference of a certain species for burns was calculated as the number of individuals at burned plots over the total number from all plots. The numbers of specimens from each guild was compared between bogs and pine ridges.

Results

Fifty species were taken from burns, and 45 species collected from control plots (Table I). The individual species in each guild and their localities in burns, controls and/or both plots are listed in Table II.

In the erigonid-linyphiid guild, those species numerous in burns include *Erigone atra* Blackwall, *Pocadicnemis americana* Millidge, *Tunagyna debilis* (Banks) (all in the family Erigonidae) and *Bathyphantes pallidus* Banks (Linyphiidae) (Table II), although 24 species in total occurred in burns. In control plots 16 species were collected, seven being possible climax species, and only in undisturbed control plots. Numbers were too low to verify such a classification. The six eurytopic or plastic species collected from both plot types were *B. pallidus*, *Meioneta simplex*

TABLE II. Spider species in different guilds and their presence in burnt, unburnt (control) and/or both plots at Taiga Biological Station, Manitoba.

Burnt	Both	Unburnt
E-L: Erigonidae-Linyphiidae Guild:		
Agyneta olivacea (Emerton)		
	Bathyphantes pallidus (Banks)	
		Ceraticelus fissiceps (O.P.-Cambridge)
		Ceratinella sp.
Centromerus longibulbus (Emerton)		
Dicymbium elongatum (Emerton)		
Eperigone trilobata (Emerton)		*Eperigone undulata* (Emerton)
Erigone atra Blackwall		
Gnathonaroides sp. n.		
Lepthyphantes complicatus (Emerton)		*Lepthyphantes zebra* (Emerton)
		Lepthyphantes sp.
Lophomma sylvaticum (Emerton)		
	Meioneta simplex (Emerton)	
Neriene radiata (Walckenear)		
Oedothorax trilobatus (Banks)		
	Pocadicnemis americana Millidge	
	Sciastes truncatus (Emerton)	
Scotinotylus pallidus (Emerton)		
Tapinocyba sp.		
	Tunagyna debilis (Banks)	
Vermontia thoracica (Emerton)		
		Wabasso cacuminatus Millidge

TABLE II - continued.

Burnt	Both	Unburnt
E-L Guild (cont'd):		
	Walckenaeria atrotibialis (O.P.-Cambridge)	
Walckenaeria castanea (Emerton)		*Walckenaeria directa* (O.P.-Cambridge)
Walckenaeria exigua Millidge		
Walckenaeria spiralis (Emerton)		
two undetermined erigonids		two undetermined erigonids
L: Lycosid Guild:		
	Alopecosa aculeata (Clerck)	
Arctosa alpigena (Doleschall)		
		Hogna frondicola (Emerton)
	Pardosa hyperborea (Thorell)	
	Pardosa mackenziana (Keyserling)	
	Pardosa moesta Banks	
	Pardosa xerampelina (Keyserling)	
	Pirata bryantae Kurata	
	Pirata insularis Emerton	
	Pirata minutus Emerton	
	Trochosa terricola Thorell	

TABLE II - continued.

Burnt	Both	Unburnt
C: Other Cursorial Species Guild:		
	Drassodes neglectus (Keyserling)	
	Gnaphosa microps (Holm)	
	Gnaphosa muscorum (L. Koch)	
Haplodrassus hiemalis (Emerton)		*Haplodrassus eunis* Chamberlin
		Herpyllus ecclesiasticus Hentz
	Micaria pulicaria (Sundevall)	
	Zelotes fratris Chamberlin	
	Agroeca ornata Banks	
Phrurotimpus borealis (Emerton)		
	Scotinella pugnata (Emerton)	
	Agelenopsis utahana (Chamberlin & Ivie)	
	Cicurina brevis (Emerton)	
	Coras montanus (Emerton)	
		Cybaeota calcarata (Emerton)
		Antistea brunnea (Emerton)
		Hahnia cinerea Emerton
	Neoantistea agilis (Keyserling)	
Ozptila sincera canadensis Dondale & Redner		
Xysticus obscurus Collett		
Tibellus oblongus (Walckenaer)		
Neon nellii Peckham & Peckham		
		Tutelina similis (Banks)
Callioplus euoplus Bishop & Crosby		*Lathys pallida* (Marx)

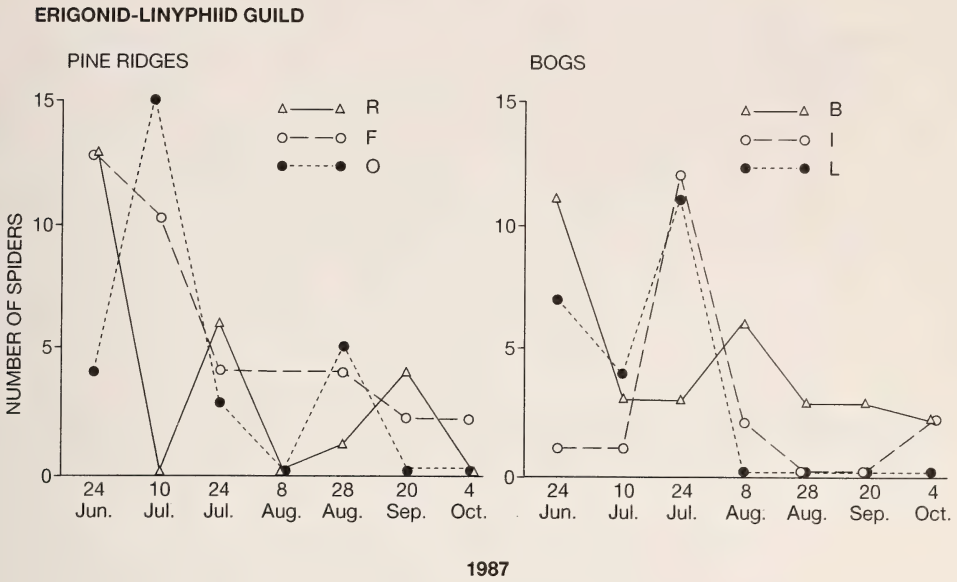

FIGURE 1. Number of spiders of the erigonid-linyphiid guild caught on pine ridges and in bogs over time. R = control pine ridge; F = freshly burnt pine ridge; O = old burn on pine ridge; B = control black spruce bog; I = intensely burnt bog; and L = lesser burnt bog.

(Emerton) (Linyphiidae), *P. americana*, *Sciastes truncatus* (Emerton) (Erigonidae), *T. debilis* and *Walckenaeria atrotibialis* O.P.-Cambridge (Erigonidae) (Table II).

In the lycosid family guild, only *Arctosa alpigena* (Doleschall) could be considered an exclusively "pioneer" species, only collected in burns, while *Hogna frondicola* (Emerton) occurred only in control plots, a possible climax species (Table II). Nine species were collected from both burns and control plots, with the dominant pioneer species in early summer being *Pardosa xerampelina* (Keyserling) and *Pirata insularis* Emerton (Table II).

In the cursorial guild, a total of 17 species were trapped, with seven occurring only in burns, all possible pioneer species (Table II). Eleven species occurred in all plots, with *Gnaphosa microps* Holm (Gnaphosidae) and *Neoantistea agilis* (Keyserling) (Hahniidae) collected mostly from undisturbed control plots; in contrast, autumn-reproducing, eurytopic *Agroeca ornata* Banks (Liocranidae) and *Zelotes fratris* Chamberlin (Gnaphosidae) were common to burns. The seven species from control plots were also possible climax species, e.g. *Herpyllus ecclestiasticus* Hentz (Gnaphosidae) (Table II).

The numbers of individuals from the erigonid-linyphiid guild in all plots are presented in Figure 1. Catches of that guild peaked in late June-early July on all jack pine ridge plots, and in late June to late July on all black spruce bog plots. Disturbed plots displayed later peaks. Catches were high in late June on both control plots (B and R) and fell from August to October (Fig. 1). Various species of erigonids and linyphiids were moderately numerous in burns, i.e. *E. atra*, *P. americana*, *T. debilis* and *B. pallidus*. Spiders of this guild showed less seasonality and therefore were trapped throughout the trapping period of June to October. *T. debilis* comprised 18.8% of the total catch from I in early August. Those families with many species displayed no real trends of dominance in either burnt or control plots.

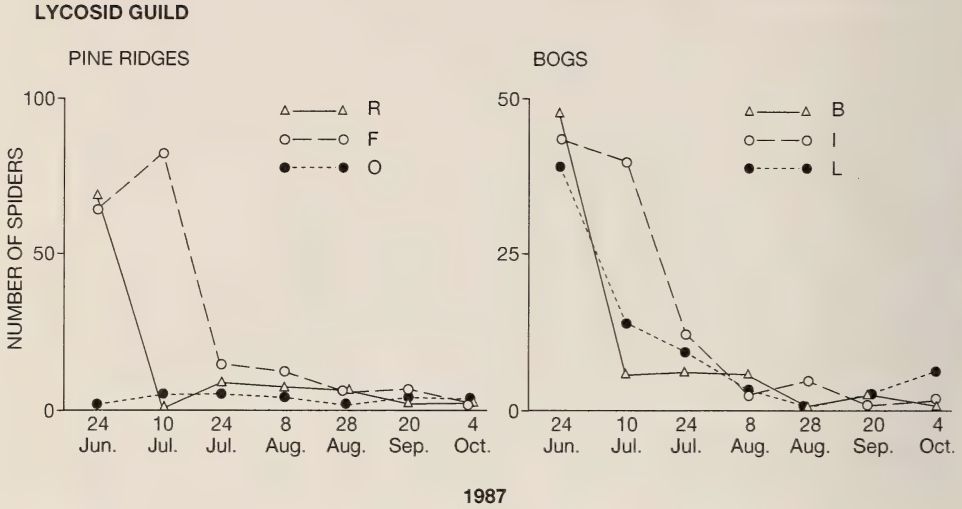

FIGURE 2. Number of spiders of the lycosid guild caught on pine ridges and in bogs over time. Abbreviations as for Figure 1.

The numbers of individuals from the lycosid guild on all plots are presents in Figure 2. All species, with the exception of *Trochosa terricola* Thorell, were predominantly active in June and July, with numbers peaking late June and early July in all plots other than O. More individuals were collected in the pine ridges than in the bogs (Fig. 2). In early July, *P. xerampelina* accounted for 88.9% of the total number of spiders from I but only 24.0% from L. By the end of August that species was no longer collected in the pitfall traps, while *T. terricola* accounted for 50.0% of the total catch (10) from F in late September.

The number of individuals from the cursorial guild are presented in Figure 3. Numbers were high at B and O in early June, especially of *G. microps*, and on R high in late June. In all the bogs, numbers dropped later in summer, while they fluctuated on the ridges. *G. microps* constituted 88.2% of the total catch from B in early July, but only 8.9% from I, and 16.0% from L, apparently dominant in and preferring undisturbed bog habitats. Another abundant species was the hahniid *N. agilis*, comprising 45.0% of the total catch from O in early June and 67.9% from the same plot in late August, but not found in recently burnt plots.

The total number of spiders collected from each plot during the study period varies from a low (150) in the intensely burnt bog to a high (226) on the freshly burnt pine ridge. The control plots were not consistently higher in numbers (215 from the bog and 188 from the pine ridge); the great mobility of lycosid pioneers at the freshly burnt pine ridge probably explains its high numbers.

Table III shows the preference for burned plots by certain species in pitfall trap material from those plots; those species compromised the pioneer group in this study. *P. xerampelina* exhibited a total preference for burns in June and July, and a strong preference in August, *E. atra* a total preference in June and a weak one later, while *A. aculeata*, *Pardosa hyperborea* (Thorell), *P. mackenziana* (Keyserling), *P.*

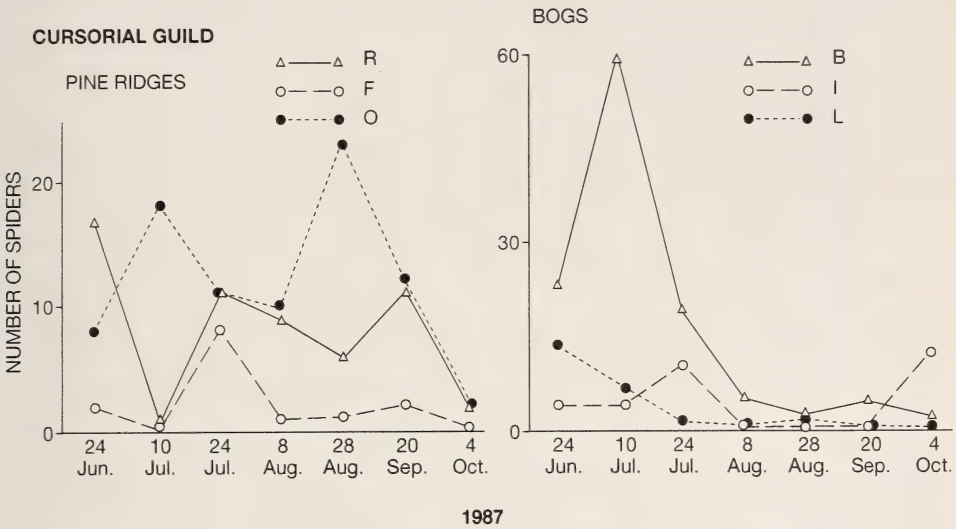

FIGURE 3. Number of spiders of the cursorial guild caught on pine ridges and in bogs over time. Abbreviations as for Figure 1.

TABLE III. Preference of certain pioneer species in pitfall trap material collected from burnt plots at Taiga Biological Station, Manitoba. N is the total number of individuals for each species at all sites throughout the study period. Percentage refers to the number of individuals at burned plots over the total number from all plots.

Species	Percentage at burn	N
Pardosa xerampelina	95.8	240
Alopecosa aculeata	100.0	12
Pardosa hyperborea	41.7	12
Pardosa mackenziana	78.6	14
Trochosa terricola	100.0	4
Agroeca ornata	50.0	4
Tunagyna debilis	100.0	7
Pocadicnemis americana	100.0	8
Erigone atra	90.0	10

moesta Banks, *A. ornata* and *P. americana* showed strong preferences for burns in June. In July, *A. ornata* and *G. microps* displayed strong preferences for burns.

Discussion

During early succession with little vegetation (one month post-fire) and much bare ground, charred down to 10 cm below the surface, the pioneer species invade a burn from adjacent undisturbed areas up to 30 m away. Those opportunistic pioneers include the lycosids (*Pardosa lugubris* (Walckenaer) and *T. terricola*) (Uetz 1979; Schaefer 1980; Bultman and Uetz 1982; Winter *et al.* 1983; Aitchison-Benell 1994) various linyphiids and erigonids (*Meioneta agrestris* (C.L. Koch), *E. atra*, *E. dentipalpis* (Wider), *Centromerita bicolor* (Blackwall)) (Huhta 1971; Duffey 1978; Schaefer 1980; Hauge and Kvamme 1983; Winter *et al.* 1983), assorted other spiders (*Coelotes terrestris* (Wider) (Amaurobiidae), *Phidippus* spp. (Salticidae), *Tibellus oblongus* (Walckenaer) (Philodromidae), *Tmarus angulatus* (Walckenaer) (Thomisidae) and *Araneus pratensis* (Hentz) (Araneidae) (Riechert and Reeder 1972; Schaefer 1980; Weaver 1985; Aitchison-Benell 1994), the collembolan *Bourletiella hortensis* (Fitch) (Winter *et al.* 1976; Tamm 1986), coleopteran lathridiids, dipteran ephydrids (Winter *et al.* 1976) and chilopods (Fellin and Kennedy 1972). There are some pyrophilous species which are attracted to fires, e.g. "smoke flies" (cerambycids) and wood-boring beetles (bupretids) (Danks and Foottit 1989), some carabid beetles (Winter *et al.* 1976; Richardson and Holliday 1982; Holliday 1984), and some weevils (*Hylobius abietis* (L.)) (Winter *et al.* 1976; Solbraa 1979). Likewise xerophilic species, such as lycosids, are often pioneers, best suited for bare habitats with sparse litter (Bultman and Uetz 1982); Huhta (1971) also determined that many spider species collected in the first four years post-fire were xerophilic. In this study those species designated as pioneer species certainly could tolerate dry habitats, e.g. lycosids *Pardosa* spp., *A. aculeata* and *T. terricola*, the clubionid *A. ornata* and the erigonid *E. atra*. Other pioneer species from Manitoba taiga included the erigonids, *P. americana*, *T. debilis* and the linyphiid *B. pallidus*.

In contrast, in late succession or in a climax situation, other species requiring phytophagous prey, much litter, or habitats with abundant vegetation and high humidity, constitute the climax fauna. They include linyphiids (*Stemonyphantes blauvelta* Gertsch, *Centromerus incilius* (L. Koch)., *Wideria fugax* (O.P.-Cambridge), *Macrargus rufus* (Wider)); erigonids *Tapinocyba pallens* (O.P.-Cambridge), *Diplocentria bidentata* (Emerton) and *Paroligolophus agrestris* (Meade) (Huhta 1971; Schaefer 1980; Hauge and Kvamme 1983; Weaver 1985); clubionid *Clubiona kastoni* Gertsch (Weaver 1985); hahniid *N. agilis* (Bultman and Uetz 1982); lycosid *Pardosa distincta* (Blackwall) (Riechert and Reeder 1972); and various epigean collembolans (*Tomocerus vulgaris* (Tullberg), *Isotoma viridis* Bourlet and *Isotomurus palustris* (Müller)) (Tamm 1986). In Finnish coniferous forests the erigonid *T. pallens* is such a dominant species (Huhta 1971), that it hardly reacted to clear-cutting and compromised 30 to 70% of the total catch (Huhta 1971). In Manitoba taiga the erigonids and linyphiids certainly were more diverse in control plots but low numbers prevented designations as climax species. *H. frondicola* was collected only from control plots, and *G. microps* and *N. agilis* mainly from control plots, potential climax species.

Some species are eurytopic in their choice of habitats and are apparently unaffected by a disturbed habitat. Huhta (1971) found *T. pallens* so abundant in all sites that its presence skewed data considerably. Riechert and Reeder (1972) found *H. frondicola* associated with dense ground cover on burnt and control sites. However, in this study *H. frondicola* occurred only at control plots. Twenty-six species from Manitoba exhibited eurytopic habits, e.g. *P. americana*, *T. debilis*, several *Pardosa* and *Pirata* spp.

Although this only covers one year and is not a successional study, some aspects of such studies will be mentioned. Species abundance, likewise, may change after a fire, with some species very abundant in early succession and declining over time as the environment becomes more complex (Duffey 1978;

Bultman and Uetz 1982). Some forest insects decrease in numbers after a fire (Fellin and Kennedy 1972; Solbra 1979). For example, Tamm (1986) found that most collembolan species decrease for up to five years post-fire, although two species were abundant in both burn and control sites. Huhta (1971) noted that the total density of spiders dropped by 60% after fire, with reduced numbers for two years afterwards; full recovery of populations too 7 to 13 years post-fire (Huhta 1971). Uetz (1979) and Bultman and Uetz (1982) found that in later succession the relative abundance of lycosids decreased, that of clubionids, thomisids and gnaphosids increased with increased litter (Uetz 1979), and that of vagrant web-builders (agelenids and hahniids) increased as the vegetation returned (Bultman and Uetz 1982). In this study at one date only was the number of lycosids higher in burns than on the pine ridges (Fig. 2), while that of the cursorial guild was low in bog burns but oscillating on pine ridges (Fig. 3). Likewise the erigonid-linyphiid guild numbers were generally high in early summer on the pine ridges and dropped later, providing no clear trends.

In northern Quebec, species found only in or mostly in burns are listed as *A. aculeata*, *P. americana*, *P. hyperborea*, *T. terricola* and *G. microps* (Koponen 1993); these are all species which had similar habitat preferences in my study. Interestingly enough, Koponen (1993) found *P. moesta* only in a control site, while in this study the species displayed a moderately strong preference for a burn site. Also the linyphiid *Lepthyphantes complicatus* (Emerton) was found only at a control site in Quebec (Koponen 1993), while it was only on burns in Manitoba. Both in Manitoba and Quebec, *Antistea brunnea* (Emerton) (Hahniidae) was collected from control plots. One pioneer species in both provinces is *A. alpigena*. Thus we can see preferences for burns by some species and eurytopism in other species.

More studies need to be conducted in the North American taiga to have conclusive data with regards to pioneer and climax species. That is particularly evident because while Koponen's study (1993) on burns in subarctic forest in Quebec corroborated much of the Manitoba data, it also showed substantial differences in the preferences of some species.

Acknowledgements

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DISTRIBUTION OF ONTARIO STONEFLIES (PLECOPTERA)

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Abstract *Proc. ent. Soc. Ont.* 125: 43-66

The historical development of the study of Plecoptera in Ontario is reviewed together with the work of the entomologists who pioneered these investigations. Current knowledge on the order is summarized and a list of the 78 species known from the province is provided with data on their distribution on a county/district basis. A number of additional species are expected, since very little systematic collecting has been conducted in most areas.

The Ontario stonefly fauna contains five zoogeographical elements: (1) a northwestern element of western origin containing three species, *Nemoura arctica*, *Isoperla decolorata*, and *Claassenia sabulosa*, the first of which is holarctic; *Isoperla citronella*, an endemic species from the northern lowlands, probably also belongs here; (2) a Great Plains species, *Isoperla longiseta*, of uncertain status; (3) a southern element of five species, *Allocapnia rickeri*, *A. vivipara*, *Clioperla clio*, *Isoperla decepta*, and *Taeniopteryx metequi*, typical of the American Midwest, inhabiting the southern lowlands; (4) an eastern element of eight species of Appalachian origin (*Acroneuria carolinensis*, *Allocapnia granulata*, *A. recta*, *Allonarcys biloba*, *Alloperla idei*, *Amphinemura nigritta*, and *Suwallia marginata*); and (5) the "Great Lakes-St.Lawrence" group forming the bulk of the fauna.

Species compositions also are given for stonefly associations from headwater, mid-size, and large running water habitats, as well as from lakes. Distinctive faunas were found to inhabit the hard-water and soft-water systems.

Perla sonans Newport 1851 is a *nomen nudum*. The Barnston specimen so labelled is *Acroneuria lycorias* (Newman 1839) rather than *A. abnormis* (Newman 1839).

Historical

The first student of stoneflies in what is now Ontario was George Barnston, an employee of the Hudson's Bay Company who rose to be an officer of the highest rank, Chief Factor. During 1836-1840, he was stationed at the St. Martin's Falls post on the Albany River (Fig. 1, #2). There, he collected botanical and zoological specimens of many sorts, which can still be found in at least three museums of natural history. He may have had a special interest in stoneflies, for he studied, named and described them, but this work was never published under his name. In 1844

FIGURE 1. Map of Ontario showing the six drainage systems in which stoneflies have been studied more intensively: 1. Winisk River; 2. Albany River; 3. Madawaska River; 4. Noisy, Mad, and Pine Rivers; 5. Thames, Nith, Grand, Speed, and Eramosa Rivers; 6. Credit River.

he presented his insect collection to the British Museum (Natural History), and seven of his stonefly species were described in papers by Newport (1848, 1851) and Walker (1852), who in some and possibly all cases used the names that Barnston had proposed: Newport states explicitly that *citronella*, *glacialis*, *minima* and *vernalis* are names proposed in Barnston's manuscript.

The published names are shown in Table I, but this is not a complete list of the species collected by Barnston. One other is "*Perla sonans*", a Barnston name that is mentioned by Newport (1851) without any description or type designation. Although this must be considered a *nomen nudum* (Ricker 1944), it was listed as a synonym of *Acroneuria abnormis* by Hagen (1861), and also by Illies (1966) and Stark and Gaufin (1976). The specimen labelled *Perla sonans* by Barnston, in the British Museum, is a female with a deformed (or partially destroyed) subgenital plate, but the absence of crossveins in the outer field of the wings indicates that it is actually *Acroneuria lycorias* (Ricker 1938, 1944). Hence if the name *sonans* is included in future species lists it should be as a synonym of *lycorias*.

During the 1850s Hermann Hagen of Königsberg in Prussia was asked by the Smithsonian Institution to prepare a review of the old Order Neuroptera in North America. His manuscript, submitted in Latin, was translated and published in 1861. The only Ontario stonefly specimens mentioned are credited to Barnston at St. Martin's Falls; they include all those in Table I, and in

TABLE I. Species whose description is based on George Barnston's specimens from St. Martin's Falls, Ontario, with the names used in the original description, and those used here.

Original	Here
Nemoura (*Brachyptera*) *glacialis* Newport 1848	*Oemopteryx glacialis*
Perla (*Capnia*) *vernalis* Newport 1848	*Capnia vernalis*
Perla minima Newport 1848	*Allocapnia minima*
Perla (*Chloroperla*) *decisa* Walker 1852	*Cultus decisus*
Perla (*Isogenus*) *olivacea* Walker 1852	*Isogenoides olivaceus*
Perla citronella Newport 1848	*Isoperla citronella*
Perla (*Isogenus*) *media* Walker 1852	*Paragnetina media*

addition he lists Barnston specimens of *Perla frontalis* Newman, of which there is one labelled "Hudson's Bay" still in the British Museum. Hagen also lists Barnston's Albany River specimens of *Pteronarcys regalis* Newman (= *P. dorsata* Say), and of *P. biloba* Newman, but the latter is presumably a misidentification. We have seen no recent stoneflies from St. Martin's Falls, but collections were made from May 31 to June 24, 1952, at Ogoki, farther down the Albany River, by J. B. Wallis. The five species obtained were *Pteronarcys dorsata*, *Isogenoides frontalis*, *I. olivaceus*, *Isoperla marlynia*, and *Acroneuria lycorias*.

Barnston evidently continued to collect natural history specimens, including stoneflies, at his later posts, but no large stonefly collection has survived. The only additional Ontario specimen that we have seen is in the Museum of Comparative Zoology at Cambridge, Mass. It is a female *Isogenoides olivaceus* from Michipicoten on Lake Superior, where he was stationed during 1859-1862.

However, George Barnston's greatest claim to fame may be that he was the first entomologist to describe the peculiar drumming habit that is widespread among stoneflies. He called his species *sonans* "the Drummer", and Newport (1851) quotes his description of this behaviour.

Despite considerable interest in entomology in Ontario and the presence of an active entomological society, it was almost 100 years after Barnston before there was any sustained activity in studying its stonefly fauna. A few specimens collected in 1903 by W.J. Wilson of the Canada Geological Survey in the Hudson Bay drainage were identified by Dr. Nathan Banks, and the names of four species subsequently appeared in the Report of the Entomological Society of Ontario (Anon. 1908). Other general collectors occasionally caught stoneflies, some of which were preserved in the collections at Ottawa, Toronto, or Guelph; but apparently Banks' (1907) Catalogue of the Neuropteroids did not stimulate special interest in the Plecoptera of the Province. Interest in two other aquatic orders, Odonata and Ephemeroptera, surfaced about 1910 at the University of Toronto and the Georgian Bay Biological Station of the Biological Board of Canada, the work of E.M. Walker and W.A. Clemens. Unfortunately the Station was on an island, and transportation both by water and by land was very restricted, so there was no chance to study running waters where stoneflies would have attracted attention.

In 1928-1930 two University of Toronto students, F.P. Ide and W.E. Ricker, were given summer employment by the Ontario Fisheries Research Laboratory to study some of the trout streams and lakes of the Province. They sampled bottom faunas in a semi-quantitative fashion, and also collected adults of most of the aquatic insect orders. Most of their work was on cuesta

streams (those flowing off the steep face of the Niagara Escarpment) in Dufferin, Grey and Simcoe Counties, not far from Georgian Bay (Fig. 1, #4), but six weeks were spent in southwestern Algonquin Park (Fig. 1, #3) which was then accessible only by railway and canoe. Ide had collected insects for the Canadian National Collection of Insects (CNCI) at Ottawa, and he soon decided to concentrate on mayflies, perhaps influenced by the fact that Dr. J. McDunnough, head of CNCI, had made them one of his specialties. With encouragement from Ide and from Dr. E.M. Walker, Ricker decided to do some systematic work on stoneflies, starting with two small papers published in 1935 (a,b). Six of the species described were from Ontario, but four of them were soon synonymized with earlier names. Dr. Ide continued working with Ontario aquatics, and during 1937-1942 used emergence traps to assess quantitatively the fauna of Costello Creek, a southern tributary of Lake Opeongo in Algonquin Park (Fig. 1, #3); the creek has its origin in Costello Lake, situated where the Opeongo Lake Road leaves the Park Highway. This creek was studied again in 1984-85, following some forest spraying in the watershed; the species obtained by Ide before and after spraying are given in Table 1 of Hall and Ide (1987).

During 1938-1941 W.M. Sprules used the emergence-trap technique at several sites in Mud Creek, a tributary of Galeairy Lake and hence of the Madawaska River in southern Algonquin Park, and also in the Madawaska River itself below the dam at Whitney, just outside the Park boundary (Fig. 1, #3). The headwaters of Mud Creek are near Costello Lake and Sprules' specimens are usually labelled "Costello Lake". His 1947 account of the stoneflies, mayflies and caddisflies is still the only semi-quantitative study of Ontario softwater streams. Dr. Sprules obtained 23 species of stoneflies, listed in his Table 12, while the seasonal emergence of six species is shown in his Fig. 9. Less extensive collections were made at other localities in and near the Park. Specimens of most or all species were sent to Dr. T.H. Frison of the Illinois Natural History Survey for identification. Specimens of all of Sprules' species have been reexamined, and the records have been included in Tables II-IV here with the name changes required by synonymy. There are also two corrections of identification. *Leuctra biloba* is an Appalachian species, and Sprules' specimens so named are *L. maria*. His *Leuctra sibleyi* must be *L. duplicata*, a common species in the Precambrian region, whereas we have not yet seen any Ontario specimens of *sibleyi*; the mistake probably stems from the misleading illustration of *sibleyi* in Needham and Claassen (1925), which has been discussed in Ricker (1965).

During the late 1940s Dr. Ide again collected in southwestern Ontario, mostly in streams near Georgian Bay (Fig. 1, #4). He also obtained (in 1946) a fine series of aquatics from emergence traps in the Credit River at Terra Cotta (Fig. 1, #6); the stoneflies were identified by Ricker and are shown in Table IV here. Ricker continued sporadic work on the classification and distribution of stoneflies through 1975, latterly in collaboration with the late Dr. H.H. Ross of the Illinois Natural History Survey and the University of Georgia. Some of these papers included records from Ontario (Ricker 1938, 1944, 1952, 1964, 1965; Ricker and Ross 1968; Ross and Ricker 1971).

In 1963 Dr. H.B.N. Hynes came to the University of Waterloo, which soon became a major centre for the study of aquatic insects, especially stoneflies. He and his students described the nymphal instars and worked out the life cycles for all the stoneflies of their region except a few very rare species (Bishop 1968; Bishop and Hynes 1969a,b; Coleman 1968; Coleman and Hynes 1970a,b; Harper and Hynes 1970, 1971a,b,c,d, 1972; Harper 1973a,b). Special attention was given to stations established on 11 clear-water streams of small to moderate size situated on the southern or southeastern slope of the highlands of southwestern Ontario (Fig. 1, #5-6), about 70 km south of the region where Ide and Ricker had worked. A total of 34 species were obtained and are listed in Table 3 of Harper and Hynes (1972).

Harper and Hynes (1972) found considerable specific and especially quantitative differences between the faunas of streams that seemed generally similar, part of which might represent year to year variability. Like Sprules, they also called attention to changes that occur in moving from cool (in summer) spring creeks to successively larger and warmer streams characterized by greater variation in volume of flow.

Other Ontario records have been published by Baumann (1974), Frison (1942), Ross and Yamamoto (1967), Ross *et al.* (1967), Stark and Baumann (1978), and Surdick (1985), but we have not searched exhaustively for records in systematic papers.

The present work brings together the distribution records based on collections made up to about 1970, with the hope that it will enhance our general knowledge of the zoogeography of the Plecoptera and stimulate further collecting throughout the Province.

Material examined

The most important collection of Ontario stoneflies is that of the Canadian National Collection (Insects) in Ottawa, which contains the specimens accumulated over the years by federal entomologists and others from all parts of Canada. Various special projects have included the Northern Insect Survey of post-war years, and a contribution to the "Winter Stonefly Project" organized by Dr. H.H. Ross during the 1960s to cover North America east of the plains (Ross and Ricker 1971). Many Ontario specimens are held in the collections of the Royal Ontario Museum, mostly taken by Dr. F.P. Ide. Other collections examined are those of the University of Guelph, McGill University (Lyman Collection, Macdonald College), the Freshwater Institute of the Department of Fisheries and Oceans in Winnipeg, the personal collection of Dr. D.M. Davies of McMaster University, and the British Museum (Natural History). Finally, a great many records are from specimens in the authors' collections.

About 800 records thus have been assembled. About a third of these are from an unpublished list compiled by Ricker in 1945, some of which have been included in the systematic and zoogeographical papers cited earlier.

Zoogeographical comments

The records presented here are too few to initiate a major discussion of the zoogeography of Ontario stoneflies. Fortunately, the faunas of most of the areas adjacent to Ontario are fairly well known: New York (Needham and Claassen 1925), Illinois (Frison 1929, 1935, 1942), Arctic Canada (Ricker 1944), Manitoba (Flannagan and Flannagan 1982), the Canadian Prairies (Ricker 1946), Minnesota (Harden and Mickel 1952), Indiana (Ricker 1945), Ohio (Gaufin 1956), and Québec (Ricker *et al.* 1968; Harper and Harper 1983), while distributions of the *Allocapnia* species throughout the whole region is discussed and pictured by Ross and Ricker (1971). It is thus possible to examine some of the general patterns of distribution and to gain some insight concerning the pathways of post-glacial dispersion of the Ontario fauna.

The distribution seems to be influenced mainly by the presence or absence of suitable habitats for the nymphs; running water is usually essential and temperature seems to be the principal regulating factor. As Ross (1963) has pointed out, the nature of the streams found in a given area depends a great deal on the riparian forest which itself is a reflection of the various geological and

FIGURE 2. Main physiographic and forest regions of Ontario. The interrupted lines separate the three major biomes, tundra, boreal forest, deciduous forest, and their ecotones; the dash-dot lines mark the Hudson Bay, Great Lakes, and St. Lawrence Lowlands; the dotted line represents the Niagara Escarpment.

climatic conditions of the area. This apparently explains the correlation of some stream insect distributions with those of major forest types.

Ontario contains three distinct terrestrial biomes (Fig. 2): the treeless tundra occurs as a narrow strip along the southern shore of Hudson Bay from the Manitoba border to Cape Henrietta Maria. At the southern tip of the Province, the deciduous forest is restricted to a band along the north shore of Lake Erie. The remainder of the Province is covered by the boreal forest and two broad ecotones, the forest-tundra transition and the boreal-deciduous forest transition (Munroe 1956). The latter is the white pine and mixed hardwood association which originally covered most of Ontario north to Timagami and Lake Nipigon, sometimes called the Great Lakes-St. Lawrence forest.

Stonefly distribution is also affected by the relief of the land which determines the presence of flowing waters and the grades of streams; most species being polyoxybiontic, stoneflies tend to be more numerous in mountainous or hilly regions. Finally, today's lowland sedimentary areas seem less favourable to some species probably because of the higher rate of siltation in the streams there, consequent on forest clearance and cultivation.

The components of the Ontario stonefly fauna are as follows:

1) **The northwestern element**: the tundra region and adjacent transition to boreal forest harbour two species found nowhere else in eastern Canada, *Nemoura arctica* and *Isoperla decolorata*, and another *Claassenia sabulosa*, that just crosses the boundary into Québec. All these have an extended distribution in the Northwest Territories. The seldom collected, and only endemic Ontario species, *Isoperla citronella*, probably belongs to this fauna also. Ricker (1964)

has postulated that, following the recession of the Wisconsin glaciation, these species dispersed eastward from a refugium in western Alaska or in the area of the present Bering Sea.

2) **The plains element**: the only characteristic Prairie species in North America is *Isoperla longiseta* Banks (Ricker 1946); though not actually recorded in Ontario, a specimen has been collected on the Québec side of the Ottawa River (Ricker 1964); it seems possible that it reached there while clinging to the side of a railway car. However, the species is widespread in Minnesota and Manitoba, so it will likely be found in adjacent Ontario localities.

3) **The southern element**: a few species typical of the American Midwest have been collected. *Allocapnia vivipara* is common throughout southern Ontario. Four others were taken in isolated localities along the Niagara escarpment: *Taeniopteryx metequi*, *Allocapnia rickeri*, *Clioperla clio*, and *Isoperla decepta*.

4) **The eastern element**: other species are widespread in the western Appalachian region and some extend more or less into the Mississippi embayment. Many of these reach their northernmost extension in southern Ontario and southwestern Québec; such are *Allocapnia granulata*, *A. recta*, *Amphinemura nigritta*, *Allonarcys biloba*, *Acroneuria carolinensis*, *A. arenosa*, *Alloperla idei*, and *Suwallia marginata*.

5) **The "Great Lakes-St.Lawrence" group** (Ricker *et al.* 1968) contains the majority of the species; these are characteristically distributed in the regions surrounding the Great Lakes. Many of them are common throughout most of Ontario; such are *Taeniopteryx burksi*, *T. nivalis*, *Leuctra ferruginea*, *L. tenuis*, *Allocapnia illinoensis*, *A. pygmaea*, *Capnura manitoba*, *Paragetina media*, *Acroneuria lycorias*, *Isogenoides frontalis*, *Isoperla bilineata*, *I. cotta*, *I. dicala*, *I. frisoni*, *I. lata*, *I. marlynia*, *I. montana*, and *I. transmarina*; some even have a transcontinental distribution: *Amphinemura linda*, *Shipsa rotunda*, *Pteronarcys dorsata*, and *Haploperla brevis*. Many species are more or less restricted to the northern parts of Ontario, while others are most often found in the southern regions. As discussed below, the distinction is due mainly to the physiographic differences between the regions. The northern section (except for the Hudson Bay Lowlands) is part of the hilly Precambrian Shield containing brown softwater streams and many lakes and bogs, whereas the southern regions are underlain by Palaeozoic sedimentary rocks, have few lakes, and the streams contain much bicarbonate and are more eutrophic. Typical species of the Precambrian highlands are *Taeniopteryx parvula*, *Oemopteryx glacialis*, *Leuctra duplicata*, *L. maria*, *Allocapnia minima*, *Capnia vernalis*, *Paracapnia opis*, *Paranemoura perfecta*, *Podmosta macdunnoughi*, *Helopicus subvarians*, *Isogenoides olivaceus*, and *Acroneuria abnormis*. Characteristic species of the sedimentary regions are *Strophopteryx fasciata*, *Isoperla nana*, *Neoperla occipitalis*, *Agnetina capitata*, *Acroneuria carolinensis*, *A. frisoni*, and *Perlesta decipiens*. A similar situation exists in Québec, where these species are distributed between the Laurentian Highlands and the St. Lawrence Lowlands (data in Ricker *et al.* 1968).

Only one of the species, *Nemoura arctica*, is holarctic. Other holarctic species, *Arcynopteryx compacta* (McLachlan), *Diura bicaudata* (L.), and *D. nanseni* (Kempny), which occur as glacial relicts in eastern North America, may eventually be found in Ontario.

Finally, a number of species not yet found in Ontario will certainly be collected there in the future. Some are indeed known from both east and west of the Province, such as *Isoperla slossonae* (Banks) and *Alloperla leonarda* Ricker. Others are members of the Appalachian fauna and have not yet been recorded, probably because of lack of collecting in the southeastern regions of Ontario. Some of them have in fact been found only a few kilometers from the border in Québec or New York: *Taeniopteryx maura* (Pictet), *Allocapnia pechumani* Ross and Ricker, *Leuctra sibleyi* Claassen, *Amphinemura wui* (Claassen), *Ostrocerca prolongata* (Claassen),

Prostoia similis (Hagen), *Paragnetina immarginata* (Say), *Perlinella ephyre* (Newman), and *P. drymo* (Newman).

Because Ontario was completely covered by the Wisconsin ice masses, the totality of species have migrated from unglaciated refugia. The influx from the west and northwest was small, and all the species involved reach their easternmost extension in Ontario or just east of its border. The major source of immigration into Ontario was probably from just south of the glaciations in the American Midwest and the western Appalachians; these species have moved north into the previously glaciated area to form the "Great Lakes-St.Lawrence" fauna. The typical Appalachian element seems to have moved northward into Québec, and from there has gradually entered Ontario. The reason for this supposition is that the area outside the Appalachian containing the richest Appalachian fauna seems to be the lower Laurentian Highlands of southern Québec; there is then a progressive decrease in the number of species westward into Ontario. A region which may harbour Appalachian species but has been rarely investigated is the Kingston area where the Canadian Shield Highlands reach the St.Lawrence River and cross it to come in contact with the Adirondack Mountains. Streams in the Great Pine Ridge along the north shore of Lake Ontario may also prove rich in stonefly species.

The Great Lakes do not seem to have been an impassable barrier to the dispersal of stoneflies, though the surrounding lowlands may have forced many less tolerant species to migrate into southeastern Ontario and into Québec before invading the upland areas north of the lakes. However, the Niagara Escarpment or Cuesta, which extends from western New York to Manitoulin Island, may have been an important dispersal route. For example, the characteristically-Appalachian species *Allonarcys biloba* and *Acroneuria carolinensis* have been taken in Ontario only in cuesta streams.

Finally, it must be stressed that, especially in the southern lowlands, the original pattern of stonefly distribution is much obscured by the growing urbanization and the development of agriculture. Except in the headwater areas and the protected sections in hilly and forested regions, many of the stoneflies have been eliminated by the pollution and the siltation of their environment.

In most cases, these ideas remain general and preliminary. Each species should eventually be studied individually, as has been done for *Allocapnia* by Ross and Yamamoto (1967), Ross *et al.* (1967) and Ross and Ricker (1971).

Comparison of hard and soft streams

Ricker (1934) made the distinction between hard or lime-rich waters and soft or brown waters a major division in his classification of Ontario streams, partly because he was impressed by the tremendous abundance of black-fly larvae (Simuliidae) in brown-water rivers like the Oxtongue. However, his faunal lists for both types of water were very incomplete; in the case of insects they were mostly based on nymphs, which were usually identified to genus at best. With the systematic and distributional information now available, a comparison of the two types has become more informative, although much remains to be done. Here we present several tables that compare the faunas of softwater and hardwater streams that are generally similar in respect to size and temperature.

Comparisons below are based on data from a variety of sources, but in all cases on a series of regular or repeated collections from one system. In some instances, quantitative data are available, either as the number of specimens caught in an emergence trap during a season (study by Sprules and unpublished data from Ide), or else as the number of nymphs collected in the

TABLE II. Species collected in spring-fed creeks of two water types. See text for streams included. Symbols and figures indicate density: 3, abundant; 2, frequent; 1, rare; +, present, but no quantitative data available; 0 or -, not collected.

	Soft waters	Hard waters
Taeniopteryx nivalis	-	1
Leuctra duplicata	3	-
L. ferruginea	3	3
L. maria	2	-
L. tenella	3	-
Paraleuctra sara	1	+
Allocapnia pygmaea	1	0-1
A. recta	+	-
Capnura manitoba	+	1-2
Paracapnia angulata	-	1-3
P. opis	+	-
Amphinemura delosa	2	} 2-3
A. linda	-	
Nemoura trispinosa	1	3
Ostrocerca albidipennis	2	-
O. complexa	+	-
O. truncata	+	-
Paranemoura perfecta	2	-
Soyedina vallicularia	-	1
Acroneuria carolinensis	-	0-1
Perlesta decipiens	-	0-1
Clioperla clio	-	0-1
Isoperla nana	-	0-1
I. orata	-	+
I. montana	2	-
I. transmarina	+	0-1
Sweltsa onkos	3	1-3

course of a one-year sampling programme (studies by Harper and Hynes). To allow comparisons, we used a numerical index to represent these data. Values range from 3 to 0, based on the following scale; [3] = abundant species (51 or more adult specimens collected in the emergence traps, or 501 or more nymphs collected in the benthos); [2] = frequent species (11-50 adults or 101-500 nymphs); [1] = rare species (1-10 adults or 1-100 nymphs); [0] = species absent from traps or benthic samples; [+] = species present, but no quantitative data available; [-] = species not collected. These symbols and figures correspond to Sprules' (1947) definitions of A(bundant), F(requent), and R(are) in his Table 12.

Spring creeks

Table II presents the faunas of spring-fed creeks of the two water types. The softwater series is mainly from Sprules' collections from emergence traps at Station 2 of Mud Creek (Fig. 1, #3). Additional records, indicated by plus signs, are from spring creeks in Maynooth in Haliburton

County, and a few from a nature trail in Algonquin Park. Records for hardwater streams are mostly from Harper and Hynes' (1972) stations 1-3: 1) headwaters of Lutteral Creek; 2) a small tributary of the Grand River; 3) a tributary of the west branch of the Speed River (Fig. 1, #5). "B" and "F" Creeks described by Ricker (1934) are of this type, and specimens were obtained from a few other spring-fed tributaries of the Noisy and Mad Rivers (Fig. 1, #4).

Table II indicates that *Leuctra ferruginea*, *Amphinemura delosa*, *Nemoura trispinosa*, and *Sweltsa onkos* are common species in at least some of the cool streams of both grades of hardness. A difference between the two types is that the soft waters have a greater variety of leuctrids and nemourids, whereas isoperlids are better represented in hard waters. Singh *et al.* (1984) monitored the emergence of a small hard-water stream along the Niagara Escarpment; their data are in general accord with our scheme, in both species composition and dominance, except that they record a large population of *Ostrocerca albidipennis*. We question, however, two of their identifications: "*Alloperla*" *lateralis* (= *Sweltsa lateralis*) is an Appalachian species previously unrecorded from Ontario and the adjoining parts of Quebec; their specimens are more probably the common *Sweltsa onkos*. *Capnia vernalis* is generally a northern transcontinental species inhabiting large rivers; its presence in southern Ontario would be quite unexpected, except perhaps as a glacial relict.

Small trout streams

The next comparison (Table III) is between streams that are somewhat larger than the spring creeks, and are considerably warmer in summer and cooler in winter, but are still suitable habitat for brook trout (*Salvelinus fontinalis* (Mitchill)) or rainbow trout (*Oncorhynchus mykiss* (Walbaum)). The softer sites included are Sprules' Stations 3 and 3A on Mud Creek, and Papineau creek near Maynooth (Fig. 1, #3). Hardwater sites include the upper sections of Hunsburger Creek (Station 4) and of the Eramosa River (Station 5) of Harper and Hynes (1972) (Fig. 1, #5) . "E" Creek and the Mad and Noisy Rivers in and near the Cuesta as described by Ricker (1934), and Ide's Silver and Black Ash Creeks near Collingwood (Fig. 1, #4).

As expected, the number of species from both types is now greater, and there is more contrast between the two. Only *Leuctra ferruginea* and *Amphinemura delosa* are abundant in both the hard and soft waters. *Allocapnia* is an important genus only in hard waters, although this superiority may be partly a result of more collecting early in the season. *Isoperla transmarina* has become an abundant species in hard waters, while *I. cotta* and *I. montana* are well represented in soft waters. *Alloperla atlantica* appears as a distinctive species of soft waters, as do *A. caudata* and *A. concolor* in the hard.

Bass rivers

Larger and somewhat warmer rivers in Ontario usually have the smallmouth bass (*Micropterus dolomieui* Lacépède) as the principal game fish, along with numerous minnows, suckers, etc. However, in softwater regions they may also contain trout; in fact Ricker's (1934) principal example, the Oxtongue River, was called a trout stream. Here this type is represented mainly by the Madawaska River below the Dam at Whitney: Sprules' Stations 4, 4A and 4B (Fig. 1, #3). Numbers in the softwater column 2 of Table IV refer to the density of adults which emerged from these stations, and the plus signs represent additional collections along that river. Hardwater streams of comparable size differ in having greater variations in volume of flow, and in carrying a much greater silt load, especially in times of flood. The best available example is the Credit River from near the Forks down to about Georgetown, where many collections have been made including Ide's at Terra Cotta (Fig. 1, #6). The hardwater column 3 of Table IV shows the

TABLE III. Species collected in small trout streams of two water types. Symbols and figures as in Table II.

	Soft waters	Hard waters
Oemopteryx glacialis	+	-
Taeniopteryx burksi	-	0-1
T. parvula	+	-
Leuctra duplicata	1-3	-
L. ferruginea	2	3
L. tenella	2	-
L. tenuis	3	-
Allocapnia minima	-	+
A. pygmaea	1	1
A. rickeri	-	+
A. vivipara	-	+
Paracapnia angulata	-	1
P. opis	+	-
Amphinemura delosa	2	} 2
A. linda	-	
Nemoura trispinosa	+	1
Paranemoura perfecta	1	-
Prostoia completa	-	0-1
Soyedina vallicularia	-	1
Agnetina capitata	-	0-1
Acroneuria abnormis	1	-
A. carolinensis	-	+
Isogenoides olivaceus	-	+
Isoperla cotta	2	0-1
I. dicala	+	+
I. frisoni	1-2	-
I. lata	+	-
I. montana	1-2	-
I. transmarina	+	2-3
Alloperla caudata	-	+
A. concolor	-	+
A. atlantica	1	-
Haploperla brevis	1	1
Sweltsa onkos	-	0-2

abundance of each species taken in Ide's emergence traps in 1946, while plus signs indicate additional species taken by others along this stretch of river.

Species that are abundant in both softwater and hardwater rivers are *Acroneuria lycorias*, *Isoperla frisoni*, *Haploperla brevis*, the late-summer species *Leuctra tenuis*, and probably *Paragnetina media*. *Amphinemura delosa* persists in the Credit but was not taken in the Madawaska. Conspicuous new occurrences are *Acroneuria abnormis* and *Isoperla lata* in the soft water, and *Agnetina capitata, Neoperla occipitalis and Alloperla banksi* in the hard.

TABLE IV. Stoneflies captured in warm bass-type rivers of two water types. Rivers are described in the text. Symbols as in Table II.

	Soft waters (Madawaska R.)	Hard waters (Credit R.)
Strophopteryx fasciata	-	+
Taeniopteryx burksi	+	-
T. nivalis	-	+
T. parvula	+	-
Leuctra ferruginea	-	+
L. tenuis	+	1
Allocapnia pygmaea	-	+
Paracapnia opis	+	-
Amphinemura delosa	-	2
Prostoia completa	-	+
Soyedina vallicularia	-	+
Pteronarcys dorsata	-	1
Agnetina capitata	-	+
Neoperla occipitalis	-	2
Paragnetina media	-	2
Acroneuria abnormis	3	-
A. carolinensis	-	+
A. lycorias	2	2
Helopicus subvarians	1	-
Isoperla cotta	-	1
I. frisoni	3	2
I. lata	2	-
I. marlynia	+	-
I. montana	-	3
I. nana	-	+
I. transmarina	2	-
Alloperla banksi	-	2
A. caudata	-	+
Haploperla brevis	1	3
Suwallia marginata	-	1

Larger rivers

The hardwater streams that descend from the highlands of southwestern Ontario become larger, muddier, and subject to extremes of temperature and volume of flow as they pass out onto a flatter and more intensively cultivated landscape. The Speed and Nith Rivers combine with the Grand to reach Lake Erie, while the Thames and its larger tributaries are of the same type (Fig. 1, #5). Somewhat smaller, but similar, are the lower reaches of the Credit River and adjacent streams flowing into Lake Ontario (Fig. 1, #6). Habitats of this sort that contribute to the hardwater column of Table V include the Nith River in Oxford County, the Grand River from Fergus south, the Speed River south from Guelph, and the Credit River from Georgetown to the lake.

TABLE V. Stoneflies collected in the larger muddy hardwater streams of southwestern Ontario, and in three large softwater rivers. Symbols as in Table II.

	Hard waters	Ottawa R.	Albany R.	Winisk R.
Oemopteryx glacialis	-	-	+	-
Strophopteryx fasciata	+	-	-	-
Taeniopteryx burksi	+	-	-	-
T. nivalis	+	-	-	-
T. parvula	-	-	-	+
Allocapnia minima	-	+	+	-
A. pygmaea	+	+	-	-
A. vivipara	+	+	-	-
Capnia vernalis	-	-	+	+
Capnura manitoba	+	-	-	-
Amphinemura delosa	+	-	-	-
Pteronarcys dorsata	-	+	+	+
Agnetina capitata	+	+	-	-
Neoperla occipitalis	+	-	-	-
Paragnetina media	+	+	+	+
Acroneuria abnormis	-	+	-	-
A. arenosa	-	+	-	-
A. frisoni	+	-	-	-
A. lycorias	+	+	+	-
Claassenia sabulosa	-	-	-	+
Perlesta decipiens	+	+	-	-
Cultus decisus	-	-	+	+
Isogenoides frontalis	-	-	+	-
I. olivaceus	-	-	+	-
Isoperla bilineata	-	+	-	-
I. citronella	-	-	+	+
I. decolorata	-	-	-	+
I. marlynia	-	+	+	-
I. montana	-	+	-	-
I. nana	+	+	-	-
I. transmarina	+	+	+	-
Haploperla brevis	-	+	-	-

There are no softwater streams closely comparable to those just mentioned because there is much less agriculture in the Precambrian country, hence there is little silt in the rivers and less seasonal variation in volume of flow. However, we present in Table V a comparison between the larger hardwater rivers and the soft Ottawa River, and also a comparison of the latter with two northern brown water rivers.

The hardwater list of Table V includes several species that occurred rarely and might have descended from smaller tributaries. Abundant were *Strophopteryx fasciata*, *Taeniopteryx burksi* and *T. nivalis*, *Allocapnia pygmaea* and *A. vivipara*, *Neoperla occipitalis*, *Paragnetina media*,

Perlesta decipiens, and *Isoperla nana*. *Acroneuria frisoni* was found only in this habitat, and for a large species it may be relatively common.

The Ottawa River at the city of Ottawa has yielded many stoneflies to the collectors of the Insect Systematics Unit of the Department of Agriculture. The species taken (Table V) are generally similar to those of the Madawaska (Table IV), but they include *Agnetina capitata* and *Perlesta decipiens*, which occur also in the hardwater rivers. The complete absence of taeniopterygids, leuctrids, and nemourids is surprising and cannot be ascribed to lack of early-season collecting because 3 species of *Allocapnia* were taken. Another significant absentee is *Neoperla occipitalis*, which occurs abundantly in the hardwater Jock River only 16 km distant. The Appalachian species *Acroneuria arenosa* is represented by a single adult individual taken in 1899; however, several were taken more recently near the Gatineau River across from Ottawa (Ricker *et al.* 1968), and it is possible the specimen came from that river.

As compared with the Ottawa River at 45° 25' N latitude, the Albany River in the region of St. Martin's Falls and Ogoki (Fig. 1, #2) is at about 51° 40' N, and the Winisk at Winisk Village lies at 55° 30'N. The two northern rivers have similar faunas, and both lack the southern elements found in the Ottawa, especially *Agnetina capitata*, *Acroneuria arenosa* and two of the *Isoperlae*. Most of the differences between the Albany and the Winisk (Fig. 1, #1) probably can be ascribed to incomplete collecting, but *Claassenia*, which is abundant at Winisk, has not yet been taken at inland sites in Ontario or Québec.

Lakes

Most stoneflies avoid lakes, but there are a few species that can live along their wave-washed shores. The commonest one in Ontario is *Acroneuria lycorias*, which is abundant in Lake Nipissing and has been taken by the shores of Lakes Superior (Thomas 1966), Muskoka, and Huron. *Neoperla mainensis* was collected in numbers near Marmora, including females emerging along the lake shore. The *Neoperlae* which are so abundant at Pointe Pelee and on the Lake Erie islands are presumably lake dwellers and may all be of this species: there is a *mainensis* specimen from Pelee Island, and another has been recorded from South Bass Island, Ohio, 10 km to the southwest (Stark and Baumann 1978). Another possible facultative lake dweller is *Isoperla bilineata*, as suggested by its occurrence on Point Pelee and by Lake Huron, and its discovery in the deep waters of Lake Superior in Wisconsin (Segelby 1974). Finally, *Arcynopteryx compacta* is a common inhabitant of lakes in the Arctic and on western mountains; its exuviae have been taken from the shore of Lake Superior, but not yet on the Canadian side.

Distribution records

A detailed list of the records, including the number of specimens, the localities, the dates, and the collector(s) has been deposited in the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Canada K1A 0S2. Photocopies or microfiche copies may be purchased on request.

The shortened version included here gives the number of records for each county or district. An arbitrary distinction has been made between the southern Counties (S) and the northern Districts (N); for more precision the subdistrict of Patricia has been treated as a district and all the records from Algonquin Park have been included under Algonquin. The extreme dates of capture of adults are also given for the two major divisions.

The order of presentation is that of Illies' (1966) catalogue; the nomenclature, however, follows recent North American usage.

The common genera *Agnetina*, *Neoperla* and *Perlesta*, which were for a long time considered monotypic in North America, have been divided over recent years. We generally have been unable to reexamine many of the older records, because the material was not kept or is otherwise unavailable; such records are therefore simply listed under the genus.

Family TAENIOPTERYGIDAE

1. *Oemopteryx glacialis* (Newport)
   S. - Grey (1), Hastings (1), April 6.
   N. - Algoma (1), Cochrane (1), Thunder Bay (10), April 11-12.

2. *Strophopteryx fasciata* (Burmeister)
   S. - Dufferin (1), Frontenac (1), Grenville (1), Grey (1), Halton (1), Hastings (3), Kent (1), Lennox and Addington (1), Oxford (1), Peel (1), Simcoe (1), Wellington (3), Wentworth (1), York (1), March 19 - June 17.
   N. - Muskoka (2), April 20.

3. *Taeniopteryx burksi* Ricker & Ross
   S. - Dufferin (5), Grey (1), Hastings (2), Renfrew (1), Simcoe (3), Waterloo (1), Wellington (1), March 15 - April 27.
   N. - Algoma (2), Algonquin (3), Muskoka (1), Nipissing (4), Thunder Bay (6), March 16 - May 2.

4. *Taeniopteryx metequi* Ricker & Ross
   S. - Halton (2), Wentworth (1), March 19 - April 4.

5. *Taeniopteryx nivalis* (Fitch)
   S. - Bruce (1), Carleton (2), Dufferin (7), Grey (13), Halton (6), Hastings (2), Peel (3), Simcoe (3), Waterloo (3), Wellington (17), Wentworth (1), York (1), March 15 - April 19.
   N. - Thunder Bay (10), April 12.

6. *Taeniopteryx parvula* Banks
   S. - Hastings (2), Renfrew (1), March 16 - April 6.
   N. - Algonquin (1), Nipissing (2), Patricia (1), Thunder Bay (7), April 6 - May 1.

Family LEUCTRIDAE

7. *Leuctra duplicata* Claassen
   S. - Dufferin (1), Haliburton (1), Hastings (1), Renfrew (1), Simcoe (1), May 28 - July 10.
   N. - Algoma (1), Algonquin (3), Parry Sound (3), May 25 - August 15.

8. *Leuctra ferruginea* (Walker)
   S. - Dufferin (3), Grey (1), Haliburton (1), Hastings (2), Ontario (1), Peel (1), Simcoe (4), Waterloo (1), Wellington (6), Wentworth (1), May 5 - October 11.
   N. - Algonquin (1), Cochrane (1), Thunder Bay (1), May 21 - August 6.

9. *Leuctra maria* Hanson
N. - Algonquin (3), Timiskaming (1), June 1-23.

10. *Leuctra tenella* Provancher
S. - Wellington (1), May 27.
N. - Algonquin (1), Muskoka (1), June 10 - July 18.

11. *Leuctra tenuis* (Pictet)
S. - Hastings (2), Peel (2), Wellington (2), June 16 - August 21.
N. - Algonquin (1), Muskoka (1), July 18 - August 8.

12. *Paraleuctra sara* (Claassen)
S. - Renfrew (1), Simcoe (2), April 20 - May 23.
N. - Algonquin (1).

Family CAPNIIDAE

13. *Allocapnia granulata* (Claassen)
S. - Carleton (2), Peterborough (1), Wellington (1), March 15 - April 28.

14. *Allocapnia illinoensis* Frison
Ross *et al.* (1967, Fig.3) indicate three records of this species from near the north and east shores of Georgian Bay.

15. *Allocapnia minima* (Newport)
S. - Carleton (1), Dufferin (1), Grey (1), Simcoe (3), March 23 - April 10.
N. - Cochrane (1), Thunder Bay (2), March 25 - April 12.
Other records in Ross *et al.* (1967, Fig. 1).

16. *Allocapnia pygmaea* (Burmeister)
S. - Carleton (1), Dufferin (6), Frontenac (1), Grey (8), Halton (2), Hastings (2), Peel (7), Renfrew (1), Simcoe (3), Wellington (9), Wentworth (2), York (2), Feb. 19 - April 21.
N. - Muskoka (1), April 8.

17. *Allocapnia recta* (Claassen)
S. - Halton (1), Hastings (3), Peel (1), Renfrew (1), Dec. 18 - March 19.

18. *Allocapnia rickeri* Frison
S. - Grey (3), Halton (1), Oxford (1), Peel (2), Simcoe (1), Wellington (2), Wentworth (1), March 19 - April 3.
Additional records mapped by Ross and Ricker (1971) in Wentworth and Oxford Counties.

19. *Allocapnia vivipara* (Claassen)
S. - Carleton (4), Dufferin (1), Grey (1), Halton (3), Lambton (2), Middlesex (1), Peel (1), Waterloo (1), Wellington (6), March 15 - April 28.

20. *Capnura manitoba* (Claassen)
S. - Renfrew (1), Waterloo (1), Wellington (4), April 2 - May 18.

N. - Algonquin (1), May 15.

21. *Capnia vernalis* (Newport)
N. - Cochrane (1), Patricia (1), April 28 - May 14.

22. *Paracapnia angulata* Hanson
S. - Ontario (1), Renfrew (1), Waterloo (1), Wellington (2), March 21 - May 6.

23. *Paracapnia opis* (Newman)
N. - Algonquin (1), Muskoka (2), April 8-20.

Family NEMOURIDAE

24. *Amphinemura delosa* (Ricker)
S. - Carleton (1), Dufferin (3), Grey (3), Haliburton (3), Halton (2), Hastings (1), Kent (1), Lincoln (1), Norfolk (4), Ontario (1), Oxford (1), Peel (2), Simcoe (5), Waterloo (1), Wellington (8), Wentworth (1), May 17 - September 4.
N. - Algonquin (2), May 28 - July 7.

25. *Amphinemura linda* (Ricker)
S. - Waterloo (1), Wellington (3), June 22 - October 4.
N. - Thunder Bay (1), Sept. 8.

26. *Amphinemura nigritta* (Provancher)
S. - Carleton (1), Haliburton (1), Halton (1), Hastings (1), May 18 - June 16.

27. *Nemoura arctica* Esben-Petersen
N. - Patricia (1); only nymphs are available, but one shows the male adult structures.

28. *Nemoura trispinosa* Claassen
S. - Brant (1), Bruce (1), Carleton (2), Dufferin (2), Grey (1), Halton (1), Hastings (2), Norfolk (1), Ontario (1), Oxford (1), Simcoe (3), Waterloo (3), Wellington (8), May 5 - August 10.
N. - Algonquin (1), Thunder Bay (1), May 28 - July 18.

29. *Ostrocerca albidipennis* (Walker)
S. - Hastings (2), Renfrew (1), May 28 - June 22.
N. - Algoma (1), Algonquin (2), May 24 - July 7.

30. *Ostrocerca complexa* (Claassen) (?)
N. Algonquin (2), May 25, females only.

31. *Ostrocerca truncata* (Claassen)
S. - Haliburton (1), Simcoe (1), May 13 - June 13.
N. - Algonquin (1), May 25.

32. *Paranemoura perfecta* (Walker)
S. - Frontenac (1), Hastings (1), Lennox and Addington (1), Renfrew (2), April 21 - May 25.

N. - Algoma (1), Algonquin (1), May 7-26.

33. *Podmosta macdunnoughi* (Ricker)
N. - Cochrane (1), May 30.

34. *Prostoia completa* (Walker)
S. - Dufferin (1), Frontenac (1), Grey (1), Peel (1), Simcoe (1), Wellington (3), April 17 - May 28.
N. - Algonquin (2), May 18-22.

35. *Shipsa rotunda* (Claassen)
S. - Carleton (2), Dufferin (1), Halton (1), Peel (1), Wellington (1), April 25 - July 1.
N. - Algonquin (2), Cochrane (1), May 30 - June 11.

36. *Soyedina vallicularia* (Wu)
S. - Dufferin (2), Grey (1), Hastings (1), Norfolk (1), Peel (2), Renfrew (1), Waterloo (1), Wellington (2), Wentworth (2), York (1), April 17 - June 20.
N. - Algonquin (1), May 2.

Family PTERONARCYIDAE
37. *Allonarcys biloba* (Newman)
S. - Halton (1), Wentworth (1).

38. *Pteronarcys dorsata* (Say)
S. - Carleton (1), Halton (1), Peel (1), Renfrew (2), Simcoe (1), May 21 - July 7.
N. - Algoma (2), Cochrane (5), Patricia (1), Thunder Bay (1), May 31 - July 20.

Family PERLIDAE
39. *Agnetina capitata* (Pictet)
For a long time the only Nearctic species recognized in this genus was *A. capitata* (Pictet), there are now three. Stark (1986) suspects that both *A. capitata* and *A. flavescens* (Walsh) occur in southern Ontario. The specimens available for reexamination have all proven to be *A. capitata.*
S. - Carleton (1), Dufferin (2), Huron (1), Peel (2), Simcoe (5), Stormont (1), Waterloo (1), Wellington (3), York (1), June 4 - July 29.

40. *Neoperla mainensis* Banks
S. - Essex (1), Hastings (1), June 21 - 29.

41. *Neoperla occipitalis* (Pictet) (= *N. freytagi* Stark and Baumann, *fide* Zwick 1987)
S. - Carleton (1), Halton (1), Peel (7), June 11 - July 8.

42. *Neoperla stewarti* Stark and Baumann
S. - Hastings (1), July 18.

Other *Neoperla* records include the following, but the specimens have not been available for reexamination since the recent revisions.
S. - Essex (1), Renfrew (1), Wellington (1), June 11 - August 18.

N. - Muskoka (1).

43. *Paragnetina media* (Walker)
S. - Carleton (5), Dufferin (5), Grey (2), Halton (6), Hastings (3), Huron (1), Leeds (1), Peel (5), Simcoe (5), Waterloo (1), Wellington (5), Wentworth (2), June 8 - Aug. 1.
N. - Algonquin (1), Cochrane (2), Patricia (3), July 18 - Aug. 5.

44. *Acroneuria abnormis* (Newman)
S. - Carleton (5), Haliburton (2), Hastings (3), Peterborough (1), Renfrew (1), June 16 - Aug. 15.
N. - Algoma (1), Algonquin (4), Cochrane (1), Muskoka (3), May 18 - Aug. 24.

45. *Acroneuria arenosa* (Pictet)
S. - Carleton (1), July 17.

46. *Acroneuria carolinensis* (Banks)
S. - Dufferin (4), Grey (1), Halton (3), Lincoln (2), Peel (2), Simcoe (2), Wellington (1), Wentworth (2), May 31 - June 29.

47. *Acroneuria frisoni* Stark and Brown
S. - Grey (1), Halton (2), Huron (2), Middlesex (1), Oxford (1), Peel (1), Simcoe (2), York (1), May 27 - July 11.

48. *Acroneuria lycorias* (Newman)
S. - Bruce (1), Carleton (3), Middlesex (1), Peel (1), Renfrew (2), Simcoe (1), York (1), May 22 - Aug. 21.
N. - Algoma (2), Algonquin (4), Cochrane (2), Kenora (1), Muskoka (3), Nipissing (1), Parry Sound (1), Patricia (1), Rainy River (1), Thunder Bay (1), May 12 - July 25.

49. *Claassenia sabulosa* (Banks)
N. - Patricia (2), July 21.

50. *Perlesta decipiens* (Walsh)
S. - Carleton (1), Grenville (1), June 22 - July 26.
Perlesta specimens not available for reexamination include:
S. - Carleton (3), Leeds (1), Wellington (2), July 22 - August 10.
N. - Kenora (1), Parry Sound (1), Aug., 21.

Family PERLODIDAE
51. *Cultus decisus* (Walker)
N. - Cochrane (2), Patricia (1), July 1-20.

52. *Helopicus subvarians* (Banks)
N. - Algoma (1), Algonquin (1), Cochrane(1), June 5 - July 20.

53. *Isogenoides frontalis* (Newman)
S. - Lincoln (2), Welland (1), May 29 - June 17.

N. - Cochrane (1), Patricia (1), Thunder Bay (1), May 31 - July 21.

54. *Isogenoides olivaceus* (Walker)
S. - Grey (1).
N. - Algoma (1), Cochrane (2), May 31 - June 2.

55. *Clioperla clio* (Newman)
S. Halton (2), Wellington (3), May 17 - June 9.

56. *Isoperla bilineata* (Say)
S. - Carleton (5), Dufferin (1), Essex (1), Grenville (1), Hastings (1), Huron (1), Kent (1), Lincoln (1), Simcoe (2), June 9 - July 28.
N. - Cochrane (1), Manitoulin (1), Rainy River (2), June 24 - July 28.

57. *Isoperla citronella* (Newport)
N. - Cochrane (1), Patricia (1), July 16.

58. *Isoperla cotta* Ricker
S. - Halton (1), Peel (2), Wellington (2), Wentworth (1), May 22 - July 9.
N. - Algonquin (1), Patricia (1), May 28 - June 21.

59. *Isoperla decepta* Frison
S. - Halton (1), May 21 - June 3.

60. *Isoperla decolorata* (Walker)
N. - Cochrane (1), July 11.

61. *Isoperla dicala* Frison
S. - Dufferin (3), Grey (1), Hastings (1), Peel (2), Simcoe (4), May 23 - July 1.
N. - Nipissing (1), Aug. 11.

62. *Isoperla frisoni* Illies
S. - Dufferin (1), Haliburton (1), Halton (2), Peel (2), Renfrew (1), Simcoe (1), Waterloo (1), Wellington (2), May 25 - July 10.
N. - Algonquin (2), Nipissing (1), Patricia (1), June 8 - Aug. 11.

63. *Isoperla lata* Frison
S. - Dufferin (1), Frontenac (1), Halton (1), Peel (1), Renfrew (1), Simcoe (2), April 21 - June 21.
N. - Algonquin (1), May 4-23.

64. *Isoperla marlynia* Needham & Claassen
S. - Carleton (2), Dufferin (1), Renfrew (1), May 12 - June 16.
N. - Algoma (1), Algonquin (1), Cochrane (1), Parry Sound (1), Patricia (1), June 2-25.

65. *Isoperla montana* (Banks)
S. - Carleton (3), Haliburton (5), Norfolk (1), Oxford (1), Peel (2), Simcoe (1), May 13 - July 5.
N. - Algonquin (1), May 26 - June 17.

66. *Isoperla nana* (Walsh)
S. - Carleton (3), Dufferin (1), Grey (1), Halton (1), Hastings (1), Kent (1), Leeds (1), Norfolk (2), Ontario (1), Peel (2), Simcoe (3), Wellington (7), May 21 - July 7.

67. *Isoperla* cf. *orata* Frison. Probably an undescribed species.
S. - Dufferin (2), Hastings (1), June 19.

68. *Isoperla signata* (Banks)
N. - Algonquin (1), June 28.

69. *Isoperla transmarina* (Newman)
S. - Carleton (1), Dufferin (2), Haliburton (1), Halton (2), Hastings (2), Lincoln (2), Ontario (1), Peel (1), Simcoe (3), Waterloo (2), Wellington (2), May 16 - June 29.
N. - Algoma (1), Algonquin (3), Cochrane (1), Kenora (1), Patricia (1), May 15 - July 10.

Family CHLOROPERLIDAE
70. *Alloperla atlantica* Baumann
N. - Algonquin (1), Parry Sound (1), June 6-22.

71. *Alloperla banksi* Frison
S. - Peel (2), May 26 - June 29.

72. *Alloperla caudata* Frison
S. - Dufferin (2), Peel (1), Simcoe (1), May 31 - July 27.

73. *Alloperla concolor* Ricker
S. - Dufferin (1), June 14-20.

74. *Alloperla idei* (Ricker)
N. - Algonquin (1), May 21.

75. *Haploperla brevis* (Banks)
S. - Carleton (2), Dufferin (2), Halton (1), Haliburton (1), Lincoln (1), Norfolk (1), Peel (2), Renfrew (1), Simcoe (4), Waterloo (1), Wellington (1), May 23 - Aug. 12.
N. - Algonquin (2), Cochrane (1), Kenora (1), Patricia (1), Rainy River (1), June 2 - July 18.

76. *Haploperla orpha* (Frison)
N. - Kenora (1).

77. *Suwallia marginata* (Banks)
S. - Peel (1), June 6-22.

78. *Sweltsa onkos* (Ricker)

S. - Dufferin (1), Hastings (1), Peel (1), Simcoe (6), Waterloo (1), Wellington (2), May 13 - Aug. 7.

N. - Algonquin (2), Muskoka (1), May 26 - July 8.

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THE INFLUENCE OF SPRAY PLACEMENT, RATE OF APPLICATION AND RAINFALL AFTER TREATMENT ON THE EFFECTIVENESS OF FOUR INSECTICIDES FOR THE CONTROL OF *PSILA ROSAE* (F.) ON CARROTS

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The efficacy of chlorfenvinphos, cypermethrin, diazinon and triazophos for the control of damage by larval *Psila rosae* (F.) to carrots was generally unaffected whether applications were directed to carrot foliage or soil along the carrot crowns. A technique using a sodium fluorescein tracer was developed, and showed that the percentage of the sprayed tracer penetrating to the soil, relative to the foliage, was as little as 5.5%. Reduction in larval mining was enhanced in foliar diazinon treatments if 1.0 cm artificial rainfall occurred within one day after treatment. Rainfall occurring two or more days following treatment did not improve control compared with foliar treatments not followed by rainfall. Diazinon sprays directed to a sandy clay loam soil were ineffective if the soil was kept dry following application.

Introduction

Larvae of the carrot rust fly, *Psila rosae* (F.) (Diptera: Psilidae), can cause serious damage to umbelliferous crops including carrots (Dufault and Coaker 1987). Although damage levels can be reduced through the use of cultural controls (Dufault and Coaker 1987), insecticide treatment is still an economic necessity for many commercial growers. In England, granular insecticides such as phorate are banded and incorporated into the soil at planting. These chemicals provide good control of first-generation larvae in May and June, but have largely degraded by the second generation in August and September (Wheatley and Wright 1970; Wheatley 1971). Most commercial carrots grown in England are left in the ground until a market is found for them, resulting in increasing damage during autumn and winter (Wright and Ashby 1946; Burn and Coaker 1981). This necessitates the use of supplementary insecticidal sprays such as diazinon during the period of second generation adult activity (Maskell and Gair 1973; Mowat and Martin 1984).

It has been suggested that granular insecticides control larvae by being translocated to feeding sites on the roots at lethal concentrations, and there is some evidence that sprayed insecticides do likewise (Wheatley and Hardman 1967; Finlayson *et al.* 1968; Suett and Whitfield 1983). Other researchers, however, have proposed that adults are the main target of supplementary sprays (Mowat and Martin 1984; Stevenson 1981). Thus, it is not clear whether larvae, adults or both are being killed following sprays, nor how sprays should be applied so as to achieve maximum

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damage reduction. Furthermore, the dense crop canopy generally present when treating for second generation *P. rosae*, and the low volume of water used as a carrier, suggest that most of the insecticidal spray falls on the carrot foliage, while the carrot crowns and surrounding soil receive little, if any insecticide (Finch 1987).

With a better understanding of these factors, commercial carrot growers could realize greater reductions in *P. rosae* damage, and possibly, a reduction in the amount of active ingredient applied. Towards these ends, this report assesses spray placement targets, application rates and rainfall following treatment for their influence on insecticidal efficacy.

Materials and Methods

General Materials and Methods and Statistical Analyses for Efficacy Studies

All experiments were performed on a sandy clay loam soil at the Cambridge University Field Station in England in 1987, 1988 and 1989. Plots consisted of six 2-m-long rows of carrots, cv. Danvers, spaced 0.33 m apart. To determine whether targeting of insecticidal sprays influenced efficacy, sprays were directed at either the foliage or to the soil along each side of the carrot crowns of each of the four middle rows. Spraying commenced at the first appearance of second generation adult *P. rosae* on yellow Correx® sticky traps (in 1987), or orange Rebell® sticky traps enclosed within Netlon sleeves (in 1988 and 1989) (Philipsen 1988). A Cooper-Pegler CP3 20 L knapsack sprayer was used; it delivered insecticides in 250 or 1,000 L water/ha at 103 kPa and was fitted with a pressure regulator, single fan nozzle and a 30 cm-wide spray shield. No insecticides were applied for control of first generation *P. rosae*. Plots were arranged in a randomized complete block and there were four replications per treatment. All carrots from the central 1-m length of the two middle rows of each plot, numbering 80-100 per plot, were harvested at season-end. They were examined for the number of mines per carrot, the most sensitive means for the comparison of treatments for damage (Dufault and Coaker 1993).

Damage data were analyzed by Genstat (Payne *et al.* 1988). The mean number of mines per carrot was calculated for each plot, and from this, the treatment means and standard errors were calculated and ANOVA performed. As some of these experiments involved structured data, orthogonal comparisons and regression analysis were also performed (Sokal and Rohlf 1981; Perry 1986). The LSD was calculated where appropriate (Sokal and Rohlf 1981; Carmer and Walker 1982; Gomez and Gomez 1984).

Where treatment means, X, exhibited variance heterogeneity, they were transformed using $\log_{10} X$, prior to ANOVA (Gomez and Gomez 1984). If any treatment means were less than one, the $\log_{10} (X + 1)$ transformation was used to eliminate negative numbers.

Spray Placement and Application Rate Studies

a) 1987 Experiment Diazinon (Basudin® 40 WP), chlorfenvinphos (Sapecron® 240 EC) and triazophos (Hostathion® (containing 420 g/L product)) were applied in 1,000 L water/ha on the dates shown in Table I at the label rates and timings recommended in England. Sprays were directed at either the foliage or to the soil along the carrot crowns. Carrots were harvested on 30 November and 1 December and evaluated for damage.

b) 1988 Experiment Diazinon was applied in 1,000 L water/ha at the full rate (2.24 kg ai/ha) to foliage and to soil, and the 1/2x, 1/4x, 1/8x, 1/16x and 1/32x rates to soil on 2 August. The UK formulation of cypermethrin (Ambush® C (containing 100 g/L formulation)) was applied at

TABLE I. Application rates and dates of insecticides applied to carrot foliage and to soil in 1987.

Treatments (kg ai/ha)	Dates Applied					
	8 Aug	22 Aug	4 Sept	18 Sept	2 Oct	21 Oct
Water-sprayed controls	x	x	x	x	x	x
Chlorfenvinphos						
2.4	x	-	-	-	-	x
Triazophos						
1.05	x	-	x	-	x	-
0.525	x	x	x	x	x	x
Diazinon						
2.24	x	-	-	-	-	x
1.12	x	x	x	x	x	-

70 g ai/ha based on the label rate for the Canadian formulation of cypermethrin (Cymbush® 250EC). Cypermethrin sprays were applied to foliage and to soil in 1,000 L water/ha on 2, 12 and 22 August and 1 and 11 September. There were two unsprayed controls, carrots from one of which were harvested on 25 August to provide a measure of first generation damage. The other unsprayed control and insecticidal treatments were harvested on 18 October to evaluate damage from the second generation.

Tracer Studies

To show whether the directed sprays employed in 1987 and 1988 were reaching the intended targets, a sodium fluorescein tracer was included in two studies. Cooke *et al.* (1986) and Çilgi and Jepson (1992), extracted sodium fluorescein from treated cereal foliage in a phosphate buffer. In the present studies, rather than attempting to recover the tracer from both soil and carrot foliage, which may have different recovery efficiencies, filter paper disks were used to capture spray droplets.

Within 1 h of treatment, petri dishes containing the filter papers were removed and enclosed in a black plastic bag, as sodium fluorescein is susceptible to photodegradation (Cooke *et al.* 1986). The dishes were returned to the laboratory where the filter papers were transferred to 20 ml vials of phosphate buffer and stored in the dark at 4°C. The phosphate buffer contained 0.1 M concentrations of di-sodium hydrogen orthophosphate dihydrate and sodium dihydrogen orthophosphate dissolved in distilled water to which the surfactant Triton X-100 was subsequently added at 0.05% (v/v) (P.S. Cuthbertson, pers. comm.).

After 24 h, the vials were warmed to 21°C for 2 h in a black plastic bag, following which the liquid contents were decanted and centrifuged at 13,000 RPM for 5 minutes. The fluorescence intensity of the resulting suspension was recorded on a Perkin-Elmer Fluorescence Spectrometer MPF-3 set to an excitation wavelength of 449 nm and an emission wavelength of 510 nm (P.S. Cuthbertson, pers. comm.) at 22°C. The phosphate buffer was used as a standard.

a) 3 September 1989 Experiment The first study, begun on 3 September 1989, examined penetration of foliar-applied sprays to soil. Four 3-cm-diameter petri dishes were suspended

horizontally immediately above the carrot foliage and four dishes were placed on the soil between the carrots along the middle 1-m length of a 2-m row of carrots in each plot. Each dish contained two 3-cm diameter filter papers. The spray mixture, which contained 2.4 g tracer and 9.0 g ai diazinon in 8.0 L water, was directed using a single nozzle at the 2-m length of foliage in each plot under still conditions at dusk. The sprays were delivered at the rate of 250, 500, 1,000, 2,000 and 4,000 L water/ha and there were four replications of each rate arranged in a randomized complete block. The eight filter papers from the foliage dishes and from the soil dishes in each plot were combined in two vials of phosphate buffer per plot.

b) 19 September 1989 Experiment The second study, begun on 19 September 1989, compared the accuracy of single-nozzle applications made to two different targets. Four petri dishes were suspended just above the crop canopy, or were placed between the carrot crowns along the middle 1-m length of a 2-m row of carrots in each plot. A single-nozzle application was directed to foliage or to each side along the carrot crowns, respectively. The spray was applied at the rate of 5 g tracer and 1.12 kg ai diazinon in 1,000 L water/ha. There were four replications of each treatment arranged in a randomized complete block. The eight filter papers from each plot were combined in one vial of phosphate buffer per plot.

Artificial Rainfall Studies With Diazinon

a) 1988 Experiment Artificial rainfall was assessed for its effects on diazinon residues on foliage. Diazinon was applied on 3 August at 1.12 kg ai/ha in 250 L water/ha to the carrot foliage in six treatments. Two h after treatment, when the spray had dried, the foliage from one treatment was sprayed with water using a back-pack sprayer. The sprayer was equipped with 4 fan nozzles delivering at 69 kPa in 100 passes at a rate equivalent to 1 cm rainfall in 5 minutes. This procedure was repeated on the other treatments 1, 2, 3, 5 and 7 days after treatment (DAT). For comparison, diazinon was also applied at 1.12 kg ai/ha on 3 August to soil in 1,000 L water/ha, and to foliage in 250 L water/ha, but not sprayed with water; there was also an unsprayed control. To achieve similar levels of soil moisture in all treatments, 1 cm water was applied on 10 August to the soil in the latter three treatments, care being taken not to wet foliage in the foliar treatment which Dufault (1992) showed could dislodge residues to the soil. Translucent polyethylene covers were laid over the treated areas on 8 August to protect residues on the foliage from removal by rainfall that occurred later that day; otherwise covers were not used during the seven days after treatment, there being no rain. A heavy dew occurred each night, however. Carrots were harvested on 18 October and evaluated for damage.

b) 1989 Experiment The influence of artificial rainfall on diazinon efficacy was further investigated in 1989. Diazinon was applied to carrots at 1.12 kg ai/ha on 17 July as follows:

- to foliage in 1,000 L water/ha; no artificial rainfall afterwards,
- to foliage in 250 L water/ha; no artificial rainfall afterwards,
- to soil in 1,000 L water/ha; no artificial rainfall afterwards,
- to foliage in 250 L water/ha; artificial rainfall afterwards, and
- to soil in 1,000 L water/ha; artificial rainfall afterwards.

Foliage in the last two treatments was sprayed with 1 cm water (as in 1988) 2 h after treatment, to compare the effects of removal of residues from the foliage or the soil surface into the soil. The first three treatments, which received no artificial rainfall, were included for comparison with artificial rainfall treatments and for comparison of the effect on efficacy of two different volumes of water used for foliar application. There was also an unsprayed control. Each

block was protected from rainfall and dew under a 4 x 6-m translucent polyethylene raincover; this was attached to a tubular steel frame and erected 2 m above the ground for two weeks after treatment. Carrots were harvested on 4 December and evaluated for damage.

Results

Spray Placement and Application Rate Studies

a) 1987 Experiment There were no differences in efficacy between foliar- and soil-applied insecticide treatments (Fig. 1). The numbers of mines per carrot from the water-sprayed controls were 2.01 ± 0.13 (foliage) and 1.55 ± 0.19 (soil), compared with the insecticidal treatments which ranged from 0.02 ± 0.01 to 0.11 ± 0.02. Orthogonal comparisons on transformed data showed that results from the ten insecticidal treatments were significantly different from the two water-sprayed controls ($P \leq 0.001$). Results from the 1x rate of chlorfenvinphos, triazophos and diazinon were not significantly different from each other, ($P > 0.05$) nor were the 1/2x rates of triazophos and diazinon significantly different from each other ($P > 0.05$). There was also no difference between 1x and 1/2x rates ($P > 0.05$). Results from each of the five foliar vs. soil insecticide treatment pairs were not significantly different ($P > 0.05$), whereas the foliar vs. soil water-sprayed controls were significantly different ($P \leq 0.005$), although this was unlikely to have been of any biological significance. Rainfall occurred 0-1 d following each insecticide application.

b) 1988 Experiment Efficacy was better in diazinon vs. cypermethrin treatments, and efficacy in soil diazinon treatments improved with increases in rate applied (Fig. 2). The numbers of mines per carrot from the unsprayed controls were 0.11 ± 0.03 (first generation), and 6.30 ± 0.65 (second generation), from diazinon 1.05 ± 0.18 (foliage) and 1.60 ± 0.18 (soil) and from cypermethrin 4.39 ± 0.42 (foliage) and 3.71 ± 0.34 (soil) (Fig. 2a). First generation damage could easily be distinguished from that caused by second generation larvae; subsequent growth in carrots between generations increased the size of mines which gained a "healed-over" appearance. The LSD ($P < 0.05$) on transformed data showed that there were significantly fewer mines per carrot in the diazinon and the cypermethrin treatments than in the unsprayed control, and that the two insecticides were significantly different from each other. There were also significant differences between the foliar and soil diazinon treatments, but not between the foliar and soil cypermethrin treatments.

The regression line in Fig. 2b showed that the numbers of mines per carrot decreased with an increase in the amount of diazinon applied to the soil. Even at 1/32x rate, there were fewer mines per carrot (5.11 ± 0.53) than in the unsprayed control (6.30 ± 0.65). Rainfall (0.4 mm) occurred immediately following application of insecticides; a further 50.2 mm fell during the following month.

Tracer Studies

In the 3 September 1989 experiment, the percentage of the sprayed tracer penetrating to disks on the soil, relative to that reaching disks above carrot foliage, ranged from 6.1 ± 1.5 (in 250 L water/ha) and 5.5 ± 1.8 (in 1,000 L) to 13.8 ± 2.3% (in 4,000 L) (Fig. 3).

In the 19 September 1989 experiment, there was no significant difference ($P > 0.05$) between sprays directed to foliage (5.2 ± 0.6 arbitrary units) vs. directed to soil along carrot crowns (5.4 ± 1.2 arbitrary units).

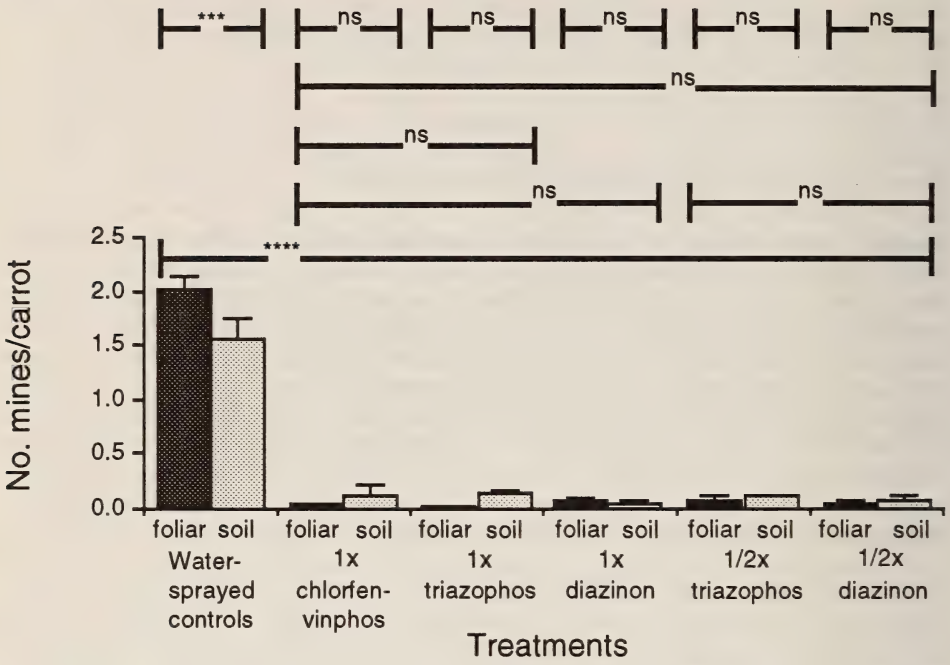

FIGURE 1. Numbers of *P. rosae* mines on carrots treated with chlorfenvinphos, triazophos and diazinon in 1987. Vertical bars are one S.E. of the untransformed mean. For orthogonal comparisons of differences in transformed data, the gap in each horizontal bar separates treatments being compared; **** = $P \leq 0.001$, *** = $P \leq 0.005$, ns = not significant.

Artificial Rainfall Studies With Diazinon

a) 1988 Experiment Rainfall increased the efficacy of diazinon treatments, but this effect diminished with time after application (Fig. 4). The number of mines per carrot in the unsprayed control was 6.53 ± 0.54 vs. diazinon without rainfall which was 4.21 ± 1.09 (soil treatment) and 4.07 ± 0.65 (foliar treatment) (Fig. 4a). The LSD ($P<0.05$) on untransformed data showed that these diazinon treatments were not significantly different from each other but that they were significantly different from the unsprayed control. In treatments in which artificial rainfall was applied to diazinon-treated foliage, numbers of mines ranged from 0.05 ± 0.01 (rainfall on day of treatment) to 3.03 ± 0.80 (rainfall 7 DAT) (Fig. 4b).

b) 1989 Experiment Rainfall increased the efficacy of diazinon-treatments vs. those not followed by rainfall (Fig. 5). The number of mines per carrot in the unsprayed control was 0.81 ± 0.11, compared with diazinon treatments without rainfall which was 0.63 ± 0.09 and 0.64 ± 0.13 (foliage treatments applied in 1,000 and 250 L water/ha, respectively) and 0.96 ± 0.18 (soil treatment).

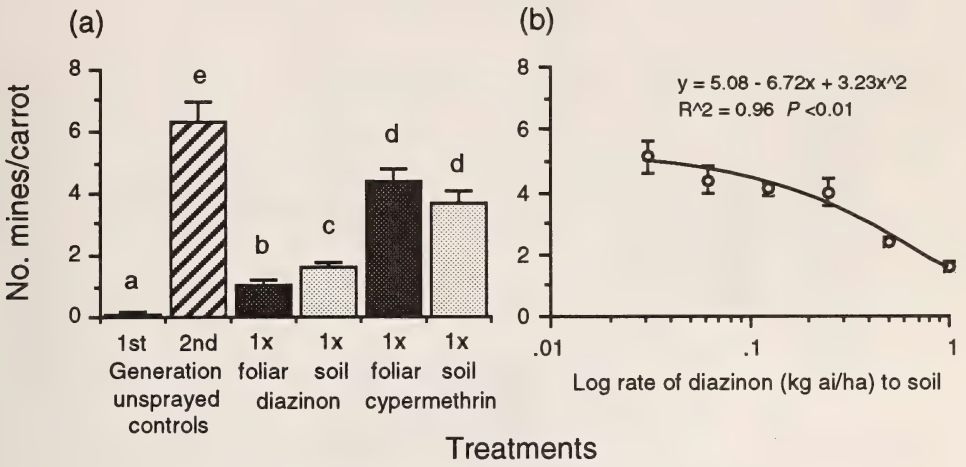

FIGURE 2. Numbers of *P. rosae* mines on carrots treated with insecticides in 1988. Vertical bars are one S.E. of the untransformed mean. (a) Compares first and second generation unsprayed controls and foliar vs. soil treatment pairs. The LSD ($P<0.05$), performed on transformed data, shows significant differences between treatments with different letters. (b) Illustrates the relationship between damage and rate of diazinon applied to soil.

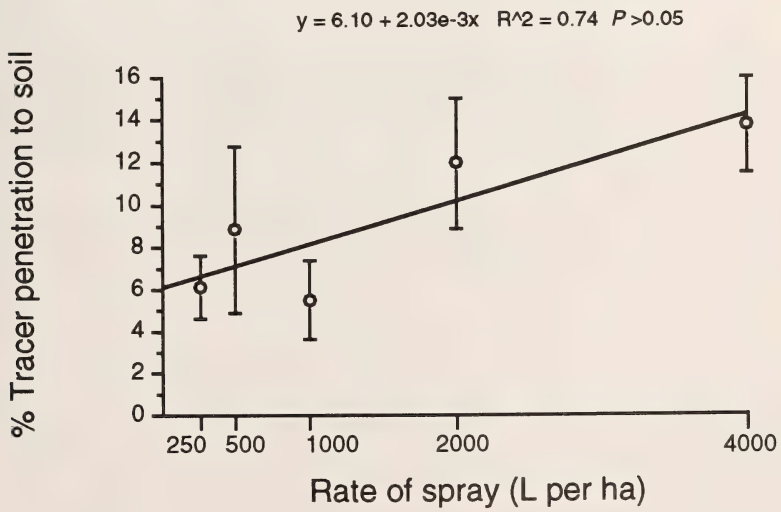

FIGURE 3. Mean % sodium fluorescein tracer penetration to soil from sprays applied to carrot foliage at different rates. The spray mixture contained 2.4 g tracer and 9.0 g ai diazinon in 8.0 L water. Vertical bars are one S.E. of the untransformed mean.

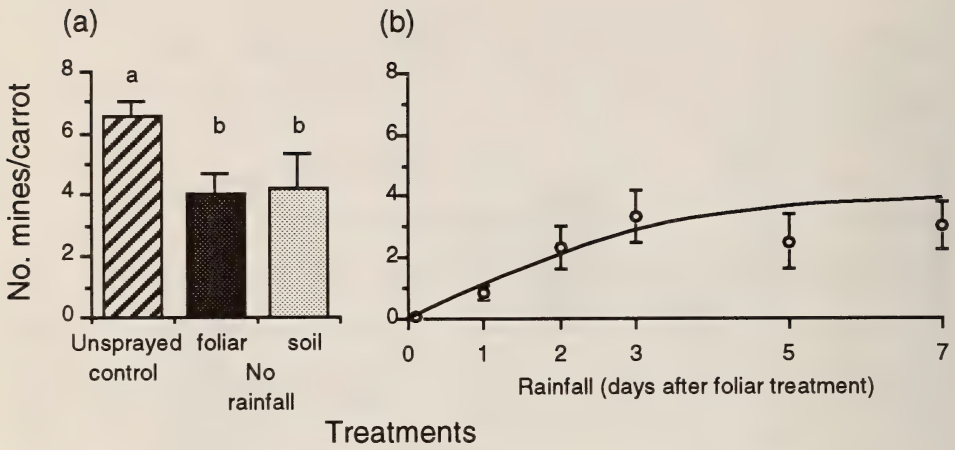

FIGURE 4. Numbers of *P. rosae* mines on carrots treated with diazinon in 1988. Vertical bars are one S.E. of the untransformed mean. (a) Compares the unsprayed control and the foliar vs. soil treatment pair without rainfall. The LSD ($P<0.05$), performed on untransformed data, shows significant differences between treatments with different letters. (b) Illustrates the relationship between efficacy and the date on which rainfall was applied after foliar treatment. Curve was drawn by hand.

With artificial rainfall, the numbers of mines were 0.03 ± 0.01 (foliage treatment) and 0.21 ± 0.05 (soil treatment). Orthogonal comparisons on transformed data showed that there were significantly fewer mines per carrot on diazinon treatments vs. the unsprayed control ($P\leq0.001$) and on diazinon treatments followed by artificial rainfall vs. treatments not followed by rainfall ($P\leq0.001$). The two foliar treatments without rainfall had significantly fewer mines than the soil treatment ($P\leq0.01$), but were not significantly different from each other ($P>0.05$). The foliar and soil treatments followed by rainfall were significantly different from each other ($P\leq0.05$).

Discussion

In the 1987 spray placement study, there was no difference between the efficacy of foliar and soil applications of diazinon, chlorfenvinphos and triazophos. In the 1988 spray placement study, however, control was significantly better with the foliar-applied, than with the soil-applied diazinon treatment, but there was no difference between cypermethrin treatments. Similarly, Maskell and Gair (1973) found significant differences in only one of eight (i.e., fenitrothion) soil vs. foliar comparisons of organophosphorous and carbamate insecticides applied for the control of *P. rosae* on carrots. Their study included chlorfenvinphos which was slightly more effective on soil vs. foliage at 1.1 kg ai/ha and on foliage vs. soil at 2.2 kg ai/ha, although these differences were not significant. The lack of significant difference in all but one foliar vs. soil treatment comparison

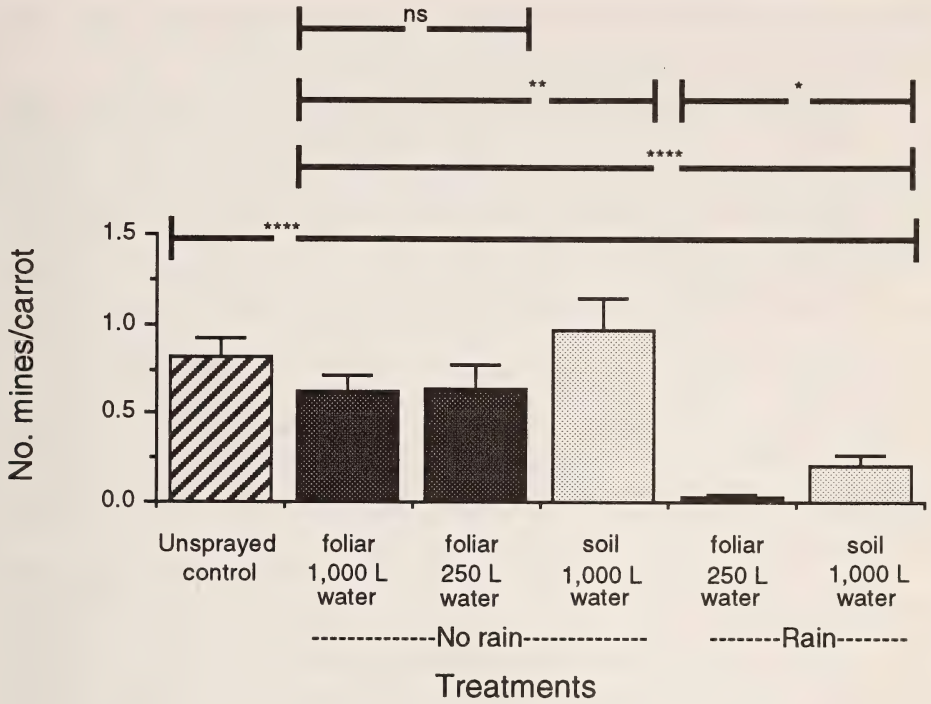

FIGURE 5. Numbers of *P. rosae* mines on carrots treated with diazinon in 1989. Vertical bars are one S.E. of the untransformed mean. For orthogonal comparisons of differences in transformed data, the gap in each horizontal bar separates treatments being compared; **** = $P \leq 0.001$, ** = $P \leq 0.01$, * = $P \leq 0.05$, ns = not significant.

at Cambridge in 1987 and 1988 suggested the need to demonstrate whether insecticides were being delivered to the intended targets and to test if rainfall could dislodge foliar residues to the soil.

The tracer study of 19 September 1989 showed that the single shielded nozzle delivered similar quantities of insecticide when targeted at foliage and at soil. The tracer study of 3 September 1989, showed that minimal foliar-applied insecticide penetrated to the soil (5.5% in 1,000 L water/ha) and that increases in penetration with increases in the rate of water, were minimal.

Results from the artificial rainfall studies in 1988 and 1989 demonstrated that efficacy increased in diazinon treatments receiving rainfall after treatment compared with treatments that did not. This suggests that diazinon was dislodged from foliage to soil where it was absorbed by carrots, thereby killing larvae feeding on peel and root hairs containing toxic residues (Wheatley and Hardman 1967). However, as diazinon movement in soil is limited (Suett 1971; Leistra *et al.* 1984), sufficient rainfall would be needed to carry residues into the soil via soil cracks for this to occur. That diazinon residues can be removed from foliage by rainfall and be absorbed by carrots at levels toxic to *P. rosae* larvae, has been demonstrated in the field and the laboratory (Dufault

1992). Other workers have demonstrated the removal of residues on foliage following rainfall with such chemicals as aldrin, azinphosmethyl, methyl parathion and malathion (Gaines and Mistric 1951; Hightower and Martin 1958; Nemec and Adkisson 1969).

The improvement in insecticidal efficacy in 1988 occurred only when artificial rainfall was applied within one day after diazinon treatment of foliage. Volatilization, photodegradation, microbial activity and retention of remaining residues may have prevented the removal of sufficient quantities of diazinon to the soil after that interval (Phillips and Gillham 1971; Hartley and Graham-Bryce 1980; Braun *et al.* 1980; Pick *et al.* 1984; McDowell *et al.* 1985; Willis and McDowell 1987).

Although removable raincovers successfully kept rainfall off treated foliage for one week after treatment in 1988, dew was formed on those nights when the covers were not used. In contrast, the permanent raincovers used in 1989 prevented dew from forming. They also had the advantages of always being in place during uncertain weather and of permitting access to carrots by *P. rosae* adults — and researchers — at all times. They may, however, have enhanced residual persistence of diazinon by reducing photodegradation (Hartley and Graham-Bryce 1980). In 1988, dew may have dislodged some of the foliar diazinon residues, a portion of which would have dripped onto the soil. This could explain the greater reduction in the number of mines per carrot in foliar diazinon treatments without rainfall vs. unsprayed controls in 1988 (38%; covers usually retracted) than in 1989 (21-22%; permanent covers).

The reduction in damage in both foliar treatments without rainfall in 1989 was likely due to adult mortality; laboratory and field studies demonstrated the toxicity of foliar diazinon residues to adult *P. rosae* (Dufault 1992). However, the similar reduction in damage (22% in 1,000 L water/ha and 21% in 250 L water/ha) was inconsistent with the increased efficacy at higher concentrations of insecticidal sprays observed by some other researchers. For example, malathion (Awad *et al.* 1967; Wheeler *et al.* 1967), acephate (Nigg *et al.* 1981) and chlorpyrifos (Veierov *et al.* 1988) were more toxic to insects exposed to foliage treated at higher concentrations, despite the same rate of active ingredient per ha being used.

In the 1989 treatments not followed by rainfall, the reductions in damage in both foliar treatments were at variance with the 19% increase in damage in the soil treatment vs. the unsprayed control. This indicated a lack of toxicity with the latter treatment to any stage of *P. rosae* and may be attributed to dry soil conditions which render diazinon non-toxic on low organic matter soils (Harris 1967; Mowat and Coaker 1967). That damage increased slightly compared with the unsprayed control, however, may have been due to toxicity to predators of *P. rosae* eggs. For example, in another experiment in the same carrot field in 1989, reduced numbers of small (i.e. <10 mm) Carabidae and of Staphylinidae were caught in pitfall traps in diazinon vs. unsprayed control plots (Dufault 1992). Similarly, Hassan (1969) observed significant reductions in numbers of Carabidae and Staphylinidae in diazinon-treated cabbage plots.

The greater reduction in the numbers of mines in foliar (96%) vs. soil (74%) diazinon treatments followed by artificial rainfall in 1989 was contrary to expectation as the amount of diazinon dislodged from foliage to soil would not have exceeded the amount sprayed onto soil. The difference may be attributed to partial adsorbance of diazinon by the dry soil (Graham-Bryce 1981) in the 2 h between the application of diazinon and of artificial rainfall. Whereas rainfall applied to treated foliage would carry the removed residues directly into the soil via soil cracks, rainfall applied to treated soil would first have to desorb residual diazinon from the soil surface before it could be carried further into the soil. Dufault (1992) showed that adsorbed diazinon was desorbed slowly from the sandy clay loam soil of the Cambridge University Field Station. As the artificial rainfall was applied for just 5 minutes, this suggests that not all of the soil-applied

diazinon was desorbed before the application of rainfall, and the movement of water carrying residues down into the soil, had ceased.

In the 1987 spray placement study, there was no difference in the efficacy of diazinon, chlorfenvinphos and triazophos, regardless of spray placement and rate applied. This suggests that chlorfenvinphos and triazophos may, like diazinon, have been dislodged from foliage to the soil by rainfall. In the 1988 spray placement study, there was no difference in the efficacy of foliar and soil cypermethrin treatments. In other laboratory and field studies, it was shown that cypermethrin was toxic to *P. rosae* adults on treated soil and foliage, however, residues in soil were not toxic to eggs and larvae, nor were residues in carrots toxic to larvae (Dufault 1992). As cypermethrin residues likely remained on foliage because they were not readily dislodged by water to soil (Dufault 1992), results from the 1988 spray placement study suggest that cypermethrin is equally efficacious on either target to *P. rosae* adults.

In conclusion, these results indicate that targeting of sprays had no impact on efficacy of insecticides for the control of *P. rosae* on carrots. Rather, in the case of the wettable powder of diazinon, efficacy was improved only if rainfall occurred within one day after treatment. Vittum (1985) applied irrigation water immediately following application of isofenphos, isazophos and diazinon for the control of grubs of *Popillia japonica* Newman in turf, thereby enhancing insecticidal activity. Similarly, results from Cambridge indicate that diazinon should be applied during, or immediately prior to rainfall or overhead irrigation, in order to achieve maximum control of *P. rosae* on carrots.

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FEASIBILITY OF DELAYING EMERGENCE OF *TRICHOGRAMMA MINUTUM* RILEY (HYMENOPTERA: TRICHOGRAMMATIDAE) AND SUBSEQUENT EFFECTS ON ADULT LONGEVITY AND FECUNDITY

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Abstract *Proc. ent. Soc. Ont.* 125: 81-86

Samples of eggs of *Ephestia kuehniella*, parasitized by *Trichogramma minutum*, were held under cool, dark conditions to determine the feasibility of delaying emergence of *T. minutum* and to assess the affect of these conditions on the reproductive performance of the emerging adults. The parasitoids were allowed to develop either at 25°C, 16L:8D, or were moved to 16°C after 3, 5 or 7 days of development at 25°C. One half of each sample moved to 16°C was held under a 12L:12D photoperiod, the other was held in the dark. The "dark" sample was held for 3 days after its paired sample started to emerge to determine if parasitoid emergence was delayed under dark conditions. Longevity and fecundity were recorded for females emerging from all rearing conditions.

Individuals from all treatments (3, 5 or 7 days at 25°C), held for an extra 3 days in darkness at 16°C, had emerged prior to removal from these conditions. Adult longevity of individuals reared at 16°C increased in direct proportion to the length of time that they were held at 16°C as pre-adult parasitoids. Rearing at 16°C reduced offspring production by *T. minutum* relative to rearing continuously at 25°C, but reproductive potential was not affected by the length of time spent at 16°C or by the light conditions (12L:12D or darkness). The results are discussed in terms of field releases of *T. minutum*.

Introduction

The spruce budworm, *Choristoneura fumiferana* (Clemens) [Lepidoptera: Tortricidae], is the most widely distributed and destructive defoliator of spruce-fir stands in eastern North America (MacLean 1985). *Trichogramma minutum* Riley [Hymenoptera: Trichogrammatidae] is a native, polyphagous, egg parasitoid that attacks the eggs of the spruce budworm (Houseweart *et al.* 1984; Pinto *et al.* 1992). Natural populations of *T. minutum* do not suppress spruce budworm populations below economic injury levels (Carrow 1990), however a research program has been undertaken to determine the feasibility of using *T. minutum* for inundative release against this pest species (Smith *et al.* 1990).

Parasitism by *T. minutum* is affected adversely by weather, with reduced emergence and very poor reproductive performance observed in cool, wet conditions (Smith *et al.* 1986). Since adverse weather conditions are frequently encountered in the field, releases may be delayed for one or several days until conditions become more suitable for the parasitoids (S.M. Smith, pers. comm.). *T. minutum* is released by aerial broadcast of dry, parasitized host eggs that are about to emerge

(Hope *et al.* 1990). Adult parasitoids cannot pass safely through the release apparatus, thus delays in application can lead to losses of adults that emerge before the parasitized material is dispersed.

Emergence of some species of *Trichogramma* can be delayed for several days, then synchronized to occur in a short period of time. Wolcott (1918) showed that emergence of some portion of a population of *T. minutum* could be delayed for 1-6 days by keeping the parasitoids in the dark. Stinner *et al.* (1974a) delayed all emergence of *T. pretiosum* Riley for 4-10 days by storing them in darkness at 16.7°C. Similar results were obtained for *T. ivelae* Pang and Chen by McLaren and Rye (1983) who found that emergence could be delayed by holding the parasitized host eggs at 15°C in the dark. In both of these cases, the majority of the parasitoids emerged in the first several hours after being restored to warm, lighted conditions. The ability to delay emergence of *T. minutum* would allow parasitized material to be held until conditions are favourable for a release, but the technique will only be of value if the reproductive performance of the parasitoids is not affected adversely by the conditions used to store them.

Our study was conducted to attempt to delay emergence for at least 3 days by holding parasitized host eggs in the dark at 16°C. A period of 3 days was chosen as an average length of time that an aerial release could be delayed in the field (S.M. Smith, pers. comm.). A temperature of 16°C was chosen as an approximate mid-point between the temperature used to delay emergence for *T. pretiosum* (Stinner *et al.* 1974a) and *T. ivelae* (McLaren and Rye 1983). We also determined the longevity and fecundity of parasitoids held at 16°C in the dark relative to those reared at 16°C, 12L:12D or at 25°C and a 16L:8D photoperiod in order to examine the effects that storage would have on the reproductive performance of the parasitoids once they emerged.

Methods

The population of *T. minutum* was originally collected by Dr. S.M. Smith (University of Toronto) from five spruce budworm egg masses on balsam fir near Quetico Park, Ontario (48.7°N 91.1°W) in July 1988. A sample of the parasitoids, reared from these initial collections, was sent to Dr. John Pinto (University of California, Riverside) for confirmation of species identity. Although *T. minutum* is currently considered to be a complex of species, the name *minutum* has been applied to all populations east of the Rockies (Pinto *et al.* 1992). The parasitoids had been in continuous laboratory culture for about 70 generations at the outset of these experiments.

Gamma-sterilized (*ca.* 60 krads) eggs of the Mediterranean flour moth, *Ephestia kuehniella* (Zeller) [Lepidoptera: Pyralidae] were exposed for 24h at 25°C to adult *T. minutum* at a ratio of *ca.* 10 host eggs per female parasitoid. After parasitism, host eggs were adhered to seven sample strips (Corrigan and Laing 1991) holding *ca.* 200 eggs per strip. The strips were put individually in cork-stoppered 3 ml vials and incubated at 25°C and a 16L:8D photoperiod. After each of 3, 5 or 7 days of development at 25°C, a pair of vials was transferred to an environmental chamber at 16°C. One vial was exposed to the 12L:12D photoperiodic regime of the chamber (3, 5 or 7 day "light" treatments) and the other was wrapped in black plastic and put in a darkened container in the chamber so that it was kept in complete darkness (3, 5 or 7 day "dark" treatments). One vial was left at 25°C, 16L:8D until the parasitoids emerged (control). The vials were moved after 3, 5 or 7 days at 25°C, 16L:8D as these times corresponded to prepupal, early pupal and late pupal development, respectively (Corrigan, unpublished). We did this to determine if the parasitoids needed to be in a particular life stage to delay their emergence. The entire experiment was replicated 4 times.

Three days after each sample held at 16°C, 12L:12D had started to emerge, the comparable sample, held in the dark, was exposed to light at 25°C and checked for emergence. Delaying emergence of the parasitoids held at 16°C, 0L:24D would be considered to be successful only if emergence of the adult wasps began after removal from the 16°C, dark conditions.

The developmental time from initial parasitism to first emergence was observed for parasitoids held at 25°C, 16L:8D and at 16°C, 12L:12D. As soon as adults were observed in each treatment, 25 female parasitoids were removed and placed individually in 3 ml vials each containing a sample strip with *ca.* 200, gamma-sterilized eggs of *E. kuehniella* to determine their longevity and fecundity. Parasitoid mortality was assessed daily, and every second day the egg strip in each vial was replaced with a fresh strip until the parasitoid died. The parasitoids were not fed. After exposure to parasitoid attack, the strips were held at 25°C, 16L:8D to allow development of the parasitoid progeny. Fecundity was measured by counting the number of blackened eggs on each strip.

Longevity, lifetime fecundity, and offspring production during the first 2 days were compared among treatments using a GLM procedure followed by a LSD multiple range test if a significant ($P<0.05$) difference was found by the GLM procedure (SAS Institute 1985).

Results and Discussion

We were not successful in delaying emergence of *T. minutum* for 3 days. In all treatments placed at 16°C, 0L:24D, adults were present upon removal of the parasitized eggs from the dark. Stinner *et al.* (1974a) reared *T. pretiosum* at 26.7°C until they had pupated and were less than 24h from emergence (8 days) then moved them to 16.7°C, 0L:24D for 4-10 days. Adults did not emerge until the parasitoids were removed from storage and transferred to daylight at 26.7°C. Similarly, *T. ivelae* that developed at 27°C, 12L:12D until the early pupal stage (6 days) could be held for an additional 6 or 7 days at 15°C, 0L:24D with emergence starting only after the parasitized eggs were placed in daylight at 23°C (McLaren and Rye 1983). The populations used by Stinner *et al.* (1974a) and McLaren and Rye (1983) originated in warmer climates (Texas, USA and Victoria, Australia, respectively) than the population of *T. minutum* used in these experiments; perhaps lower temperatures would delay emergence of *T. minutum.* Since the strips held at 16°C in the dark were not checked until 3 days after emergence of the paired samples held at 16°C, 12L:12D, it is possible that emergence was delayed, but for a period of less than 3 days.

There was a positive relationship between total immature developmental time and the amount of time that parasitized eggs were held at 16°C, 12L:12D (Table I). This result was consistent with that of Lawrence *et al.* (1985), who found that the developmental rate of *T. minutum* varied directly with temperature.

All individuals from the 16°C "dark" treatments had emerged prior to the beginning of the experiments on reproductive performance, so measurements of longevity of these individuals do not include the period of time they spent as adults in the dark. Despite this, there were no significant differences in measured longevity for adults from comparable pairs of treatments held at 16°C in the dark or at 12L:12D for 3, 5 or 7 days ($P<0.05$, LSD, Table II). Longevity of adult parasitoids from the control, the 7-day "light" and the 7-day "dark" treatments was significantly shorter than the longevity of all other treated individuals ($P<0.05$, LSD, Table II). The individuals in the 3-day "light" and the 3-day "dark" treatments had significantly longer lifespans than those in all other treatments ($P<0.05$, LSD, Table II).

TABLE I. Holding times at each temperature/light condition and total immature developmental times (mean ± SD) for samples of eggs of *E. kuehniella* parasitized by *T. minutum*.

Treatment	Holding Time (days) at		Total immature holding/development period (days)
	25°C, 16L:8D	16°C, 12L:12D	
Control (25°C continuous)	8.8 ± 0.5	0	8.8 ± 0.5
7 days at 25°C	7	5.3 ± 1.0	12.3 ± 1.0
5 days at 25°C	5	10.8 ± 0.5	15.8 ± 0.5
3 days at 25°C	3	16.0 ± 0	19.0 ± 0

It was initially expected that exposure to cool temperatures during the immature developmental period would have a negative effect on the longevity of the treated parasitoids. Stinner *et al.* (1974b) found that the longevity of fed, cold-stored *T. pretiosum*, reared from eggs of *Sitotroga cerealella* (Olivier) [Lepidoptera: Gelechiidae], was shorter than that of unstored parasitoids. Our results suggest the greater the length of time that *T. minutum* spent in cold storage as pre-adult parasitoids, the longer the post-emergent adults lived.

The lifetime fecundity of the individuals reared continuously at 25°C, 16L:8D was significantly higher than the fecundity of all other individuals except the 3-day "dark" treated parasitoids ($P<0.05$, LSD, Table II). The 3-day "dark" individuals had a significantly higher fecundity than the 7-day "dark" individuals ($P<0.05$, LSD, Table II); however, the lifetime offspring production of all other individuals held at 16°C did not differ significantly ($P>0.05$, LSD, Table II). Stinner *et al.* (1974b) found no significant differences in the number of progeny produced by *T. pretiosum* reared from *S. cerealella* whether they were unstored or stored for 4, 6, 8 or 10 days at 16.7°C.

Offspring production by females in the first 2 days was significantly higher ($P<0.05$, LSD, Table II) at 25°C, 16L:8D than at all other treatments, which were relatively similar to each other. The percentage of the total lifetime offspring production that occurred during the first 2 days was inversely proportional to the longevity of females from the different treatments (Table II). Those females that passed a greater proportion of their immature development at 16°C lived longer, therefore spreading their lifetime fecundity over a longer period of time (Table II).

The techniques tested in these experiments do not provide an answer to the problem of holding host eggs, parasitized by *T. minutum*, substantially past their normal emergence times in field release situations. Further studies need to be done to determine if there are other temperature/light conditions that would effectively delay emergence. Also, based on our results, delaying emergence by holding parasitized host eggs at low temperatures will adversely affect the reproductive performance of the parasitoids after release, yet there may be several ways that a mass-culture system for *T. minutum* could benefit from rearing some material at lower temperatures.

Low temperature rearing can increase developmental time from about 9 days up to 19 days. Increasing the developmental time means that cultures of parasitoids can be initiated earlier before a date-targeted release, effectively doubling the number of parasitoids that a factory-style, mass-rearing system can produce for the field. Under certain situations, it might be advantageous to release a mixture of adults reared at higher and lower temperatures. This would result in a "mosaic" of adult activity; some adults would provide their maximum reproductive output immediately after emergence, others would be active for longer periods of time, albeit at somewhat

TABLE II: Adult longevity in days (mean ± SD), lifetime fecundity, offspring production during the first 2 days of oviposition and percentage of lifetime fecundity produced in the first 2 days for female *T. minutum* reared from eggs of *E. kuehniella* held at 25°C, 16L:8D (control), 16°C, 12L:12D (light) or 16°C, 0L:24D (dark).

Treatment (N)	Adult longevity	Lifetime fecundity	First 2 day fecundity	Percent 2 day/lifetime fecundity
Control (98)	2.1 ± 1.0 a	59.8 ± 21.8 a	57.4 ± 18.3 a	96
7 Light (98)	2.3 ± 1.4 a	47.4 ± 29.2 bc	43.1 ± 24.6 b	91
7 Dark (98)	1.8 ± 1.3 a	42.2 ± 24.7 b	40.2 ± 21.9 bc	95
5 Light (99)	3.1 ± 1.9 b	47.9 ± 27.9 bc	39.3 ± 18.6 bc	82
5 Dark (100)	3.2 ± 2.0 b	47.7 ± 27.3 bc	38.1 ± 16.1 bc	80
3 Light (98)	3.9 ± 2.4 c	49.8 ± 30.8 bc	36.3 ± 18.6 c	73
3 Dark (98)	4.1 ± 2.5 c	52.4 ± 29.0 ac	38.8 ± 14.2 bc	74

Means in columns followed by the different letters are significantly different from each other ($P<0.05$, LSD tests).

lower levels of reproductive activity. This would extend the effective period of a field release in situations in which the host eggs are oviposited over a sustained period.

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EFFECT OF TEMPERATURE ON DIAPAUSE DEVELOPMENT IN PUPAE OF THE CARROT RUST FLY, *PSILA ROSAE* (FAB.) (DIPTERA: PSILIDAE)

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Abstract *Proc. ent. Soc. Ont.* 125: 87-93

The duration of diapause in pupae of the carrot rust fly, *Psila rosae* (Fab.), at 4 different temperatures was studied in the laboratory. Carrot rust fly larvae were obtained from carrots collected from commercial carrot fields in the Holland Marsh, Ontario, and permitted to pupate in the field in early to mid-October or at 10°C to induce diapause. Field and laboratory pupae were held at -2, 1, 5 and 7.5°C for 1, 2, 3, 4, and 5 months before transfer to 20°C. Diapause development of both laboratory and field-pupated individuals proceeded faster at 7.5 and 5°C than at 1 or -2°C. Some post-diapause development occurred at 5 and 7.5°C.

Introduction

The carrot rust fly, *Psila rosae* (Fab.), is an important pest of carrots and other Apiaceae (Umbelliferae) in most places where these crops are grown in temperate regions. This insect is often reared in the laboratory to study its response to insecticides or ecological factors, and rearing methods have been described (Stadler 1971; McLeod *et al.* 1985). Although the carrot rust fly is multivoltine, and can be reared through successive generations without diapause, an understanding of the effects of environmental factors on diapause in the insect can be important to a rearing programme. In Ontario, pupae in diapause can be collected in large numbers from heavily infested fields in late autumn to establish or replenish a laboratory colony. Moreover, intentional induction of diapause could be a useful tool in rearing. Such a method, as used successfully in rearing the cabbage maggot (Harris and Svec 1966), consists of inducing diapause in pupae and keeping them at appropriate temperatures until diapause has been terminated. Later, adult emergence can be synchronized by incubation of pupae at appropriate temperatures and times. To use either procedure effectively, it is necessary to know the effect of temperature on the duration of diapause.

The influence of temperature on the induction, maintenance, and duration of diapause in insects has been reviewed extensively (Andrewartha 1952; Tauber and Tauber 1976; Danks 1987). The induction of diapause in the carrot rust fly depends on the temperature at pupation. The incidence of diapause (proportion of individuals in the state of diapause) increases with decreasing temperature from *ca.* 15°C and reaches 100% at *ca.* 10°C (Stadler 1970; Burn and Coaker 1981; Stevenson 1981; McLeod *et al.* 1985). Once in diapause, pupae must undergo a process called diapause development (Andrewartha 1952) before morphogenesis can take place. The rate of diapause development can vary with temperature. Collier and Finch (1983) found that the rate of diapause development in the cabbage maggot, *Delia radicum* (L.), was inversely proportional to the temperature between 0 and 10°C. When carrot rust fly pupae were held at 1°C (McLeod *et al.* 1985) or 3°C (Brunel and Missonnier 1968), the time required for development of pupae on

being transferred to favourable temperatures decreased with time of exposure to the low temperature, indicating that diapause development was taking place. However, no studies comparing diapause development in a single population of the carrot rust fly at different temperatures have been reported and the study reported here was carried out with that objective.

Materials and Methods

Duration of diapause was compared at 4 temperatures, two below (-2 and 1°C) and two above (5 and 7.5°C) the threshold for pupal development of *ca.* 2°C (Stadler 1970; Stevenson 1981; McLeod *et al.* 1985), using pupae formed in both field and laboratory, but with both types originating from field-collected larvae.

The population of carrot rust fly used in these experiments was obtained from infested carrots grown in an insecticide-free planting at the Holland Marsh, near Bradford, Ontario. The carrots were taken to an outdoor insectary at Jordan Station, Ontario, and arranged so that maturing larvae could be collected, or were set up in the field at the Holland Marsh as described below. Procedures for collecting larvae, acquiring pupae, inducing diapause, incubating pupae for development to adults, and recording and processing results were described earlier (Stevenson and Barszcz 1991).

Those larvae that pupated in the laboratory were collected from the insectary, as described above, from 1 to 11 October, 1984, and placed in continuous darkness at 10±0.5°C to pupate. Pupae (hereinafter called "laboratory pupae") were divided into 4 groups of approximately 300 and placed at -2°, 1°, 5°, and 7.5±0.5°C in continuous darkness. One cohort of 50 pupae from each storage temperature was transferred to 20±0.5°C at monthly intervals for 5 months.

"Field pupae" were obtained by placing carrots, collected at the same time and location, in screen-bottomed frames mounted over other frames of the same dimensions, but with a fine-mesh screen floor and containing muck soil. The bottom frames were then placed at the perimeter of a field at the Holland Marsh and dug into the soil to help retain moisture in the recovery soil. On 14 November, pupae were collected from the soil in the lower frames, divided into equal lots, and treated as described for the laboratory pupae.

The numbers of adults emerging from each cohort of pupae were recorded at intervals of 1 to 3 days. When the interval between emergence checks was more than one day, the numbers of adults was averaged over the number of days. Data were analyzed using the GLM Procedure (SAS Institute 1985) and significantly different means (mean development time in days) identified using Tukey's studentized range test (SAS Institute 1985). For each sample, cumulative percent emergence, based on the total number of flies emerging, was calculated and plotted against time in days after placement at developmental temperatures.

Results and Discussion

Terminology of diapause has varied with different authors (Andrewartha 1952; Tauber and Tauber 1976; Danks 1987). In this paper, diapause development refers to all processes that occur from the time of diapause induction until the pupae are ready to respond to temperatures permitting normal pupal development, called non-diapause development here. Wherever we are unable to separate the two processes, we simply refer to "development". We recognize that the complete development process from formation of the pupa at a temperature inducing diapause to adult

emergence may be more complex than implied here, but further elaboration of the processes is beyond the scope of this study.

In the discussion, we assume that diapause was induced in all or very nearly all individuals by virtue of pupation at 10°C (Stadler 1970; Burn and Coaker 1981; Stevenson 1981; McLeod *et al.* 1985), as well as in those pupated in the field in mid to late-October (Stevenson and Barszcz 1989). Because it was impractical to collect individual pupae immediately after pupation, we acknowledge that some diapause development could have occurred at 10°C or in the field before pupae were placed at the storage temperatures, but all pupae used in one experiment were subject to the same factors. Pupae were considered to be in the diapause state until diapause development was completed (= diapause was terminated), as indicated by the time required until adult emergence at 20°C. Depending upon the temperature and time of storage, and given the normal variability of the population, we assume that some cohorts placed at 20°C would have included individuals in both diapause and non-diapause states.

Expected times of non-diapause development for carrot rust fly pupae to adult are about 16 to 25 days at 20°C (Brunel and Missonnier 1968; Stadler 1970; Stevenson 1981; McLeod *et al.* 1985). Burn and Coaker (1981) reported that 40 to 70 days at 20°C were required to complete diapause in the carrot rust fly. Pupae in the early stages of diapause were expected to require 30 to 60 days to develop at 20°C (Stevenson and Barszcz 1989, 1991). Because the ranges of development times of pupae nearing completion of diapause development may overlap those of non-diapause pupae, we were unable to determine the true percentage of individuals in the diapause state for all cohorts. Instead, we compared diapause status by graphing cumulative adult emergence against time, and estimated the proportion in diapause by means of a vertical line on the graph at 25 days to represent the approximate separation of diapause and non-diapause pupae.

The duration of diapause in individuals pupating at 10°C was affected by the temperature at which they were held for periods of up to 5 months (Fig. 1). Among pupae held for one month at 1°C, development at 20°C required more time for those held at 7.5 and 5°C than for those held at 1 or -2°C ($F=27.5$, $P=0.0001$). After two months, there were no differences in development times of pupae stored at the 4 temperatures ($F=1.0$, $P=0.4$). After 3 months, some of the pupae apparently had completed diapause development plus some non-diapause development at 7.5 and 5°C, as evidenced by minimum development times at 20°C of less than 15 days. However, the only significant difference observed was between pupae from -2° and 5°C ($F=3.0$, $P=0.03$). By 4 months, most pupae at the two warmer temperatures (5 and 7.5°C) had completed diapause development while there was no significant difference between pupae held at 1 and -2°C ($F=13.4$, $P=0.0001$). After 5 months, there were significant differences between the mean development times of pupae held at all 4 temperatures ($F=42.8$, $P=0.0001$), with about 50% of the pupae from -2°C, and possibly a small portion of those from the other three temperatures still in diapause. More than 50 percent of pupae at 5°C had undergone some post-diapause development by 5 months. At 7.5°C, about 24 percent of the pupae had developed to adults (development times not determined) by 5 months, so the sample set up at 20°C at that time was not totally representative of the original cohort.

The field-collected pupae (Fig. 2) generally appeared to be more advanced in development in the first three months than the laboratory pupae, possibly because some diapause development occurred in the field before they were brought to the laboratory. There were no differences in response to the 4 temperatures on transfer to 20°C at one month ($F=2.1$, $P=0.1$). After two months, pupae held at 7.5°C developed more rapidly than those held at -2 and 1°C. After 3 months, pupae held at 5 and 7.5°C developed more rapidly at 20°C than those held at -2 and 1°C, and had undergone some non-diapause development ($F=41.0$, $P=0.0001$). By 4 months, all four

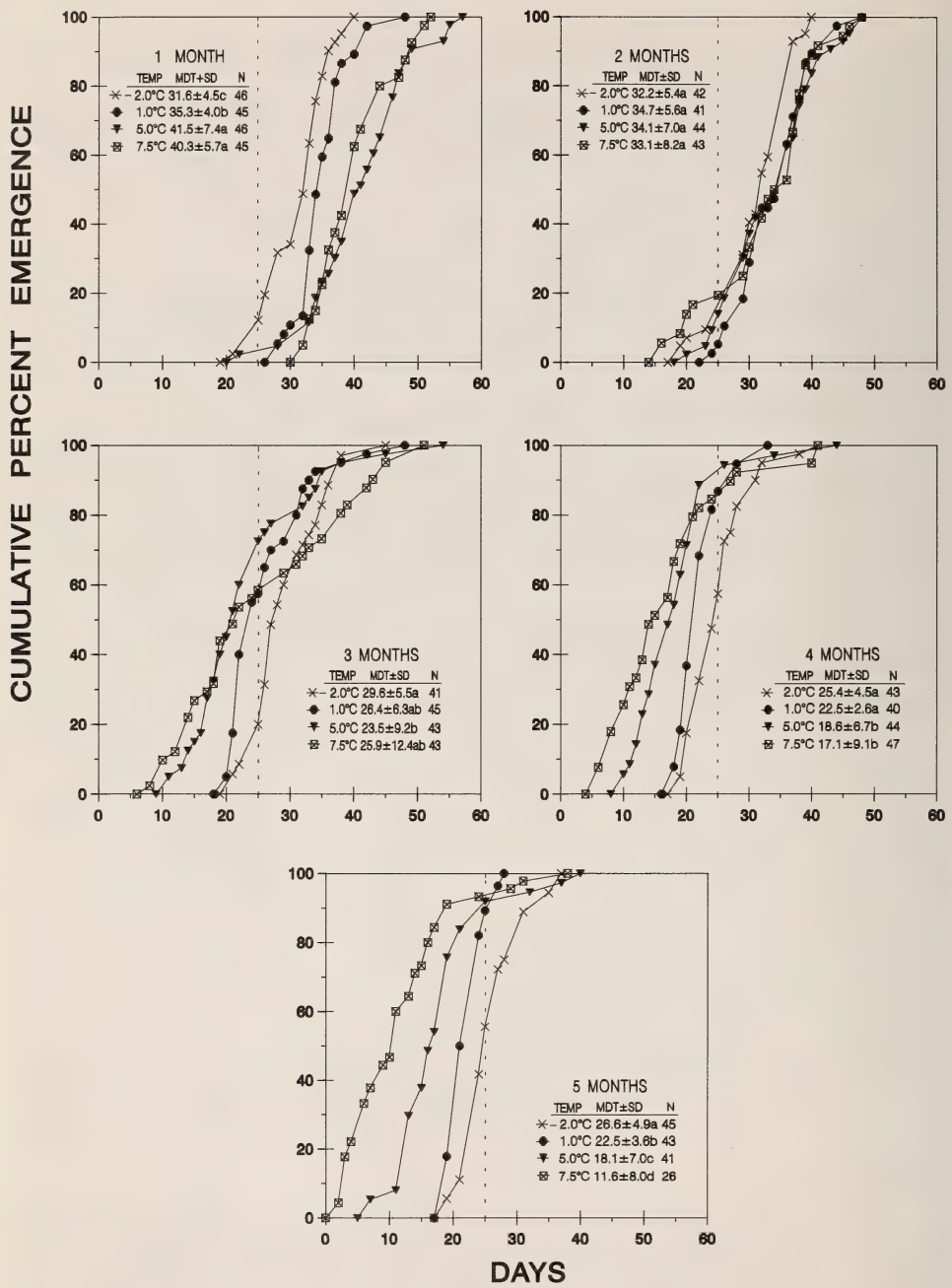

FIGURE 1. Cumulative percent emergence of carrot rust fly adults from pupae held at 4 different temperatures for 1 to 5 months after pupation at 10°C and then transferred to 20°C. Broken vertical line indicates estimated separation between diapause and non-diapause pupae.

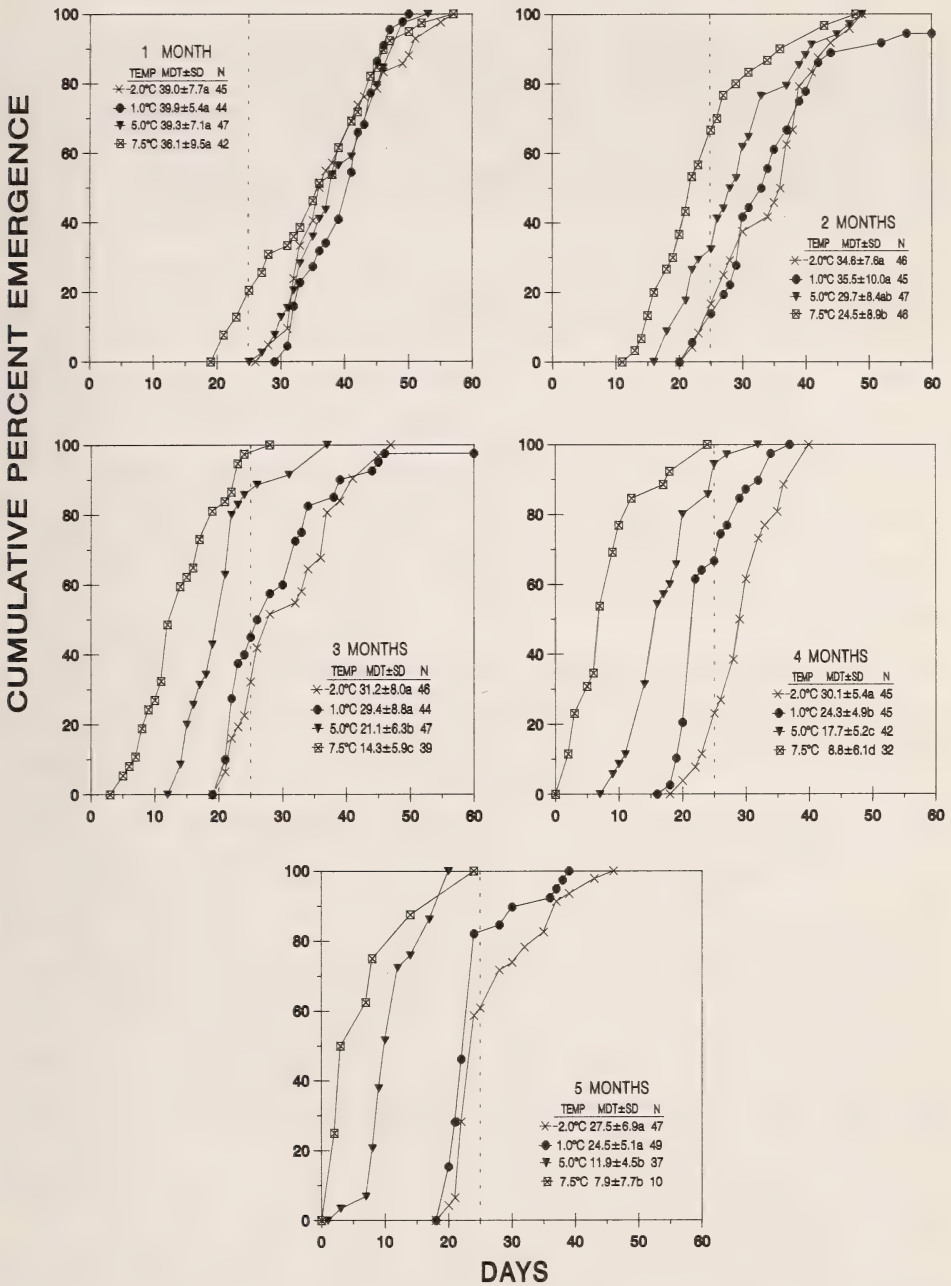

FIGURE 2. Cumulative percent emergence of carrot rust fly adults from pupae formed in the field at Bradford, Ontario, and held at 4 different temperatures for varying periods before being transferred to 20°C. Broken vertical line indicates estimated separation between diapause and non-diapause pupae.

groups of pupae had significantly different development times at 20°C (F=78.9, P=0.0001). After 5 months, there was no difference between pupae from 1 and -2°C while pupae at 7.5 and 5°C had undergone some development and emergence before transfer to 20°C (F=42.8, P=0.0001). After 4 months at 7.5°C, an estimated 4 to 8 percent of the pupae had emerged in storage, and after 5 months, only 26 pupae were recovered for transfer to 20°C, indicating that approximately 50 percent of the individuals remaining beyond 4 months had developed to the adult stage (emergence dates not determined).

The data for laboratory and field pupae at 4 temperatures were rearranged to compare development times between months for each temperature and reanalyzed in an attempt to determine when diapause development was completed at each temperature. At -2°C, 40 (field pupae) to 50 (laboratory pupae) percent of the pupae were still in diapause after 5 months. At 1°C, diapause development was completed in a majority of pupae by 4 months, but diapause persisted in 15 (laboratory) to 20 (field) percent of pupae at 5 months. At 5°C, diapause development was completed in the majority of field pupae by 3 months, but about 12 percent of the laboratory pupae were still in diapause at 5 months. At 7.5°C, no trace of diapause remained in field pupae after 4 months, but about 10 percent of the laboratory pupae were still in diapause at 5 months.

Pupal mortality, as determined by examination of the soil in the vials after adult emergence had ceased, was below 10 percent in most cohorts, but was greater than average in those kept at 5°C for 5 months (24.6%) and at 7.5°C for 4 (36%) and 5 (61.5%) months. The cause of mortality was not determined.

Diapause in both field- and laboratory-pupated carrot rust fly was shorter in duration at 7.5 and 5°C, temperatures above the threshold temperature for development of non-diapause pupae, than at the temperatures below the developmental threshold of 1.5 to 2.3°C (Stadler 1970; Stevenson 1981; McLeod *et al.* 1985). This result contrasts with that reported by Collier and Finch (1983) for the cabbage maggot, *Delia radicum* (L.), which underwent diapause development at a faster rate at lower temperatures. Therefore, in the carrot rust fly, diapause would be expected to last longer in colder climates or in the colder winters in a given location. In Ontario, the estimated proportion of overwintering pupae that were still in diapause in early April (i.e. the proportion of the pupae collected that required more than 25 days to complete development to adult) varied from year to year and the coldest of the 3 winters for which data were available was the one having the most evidence of diapause in early April (Stevenson and Barszcz 1989).

Although direct comparisons of diapause duration at temperatures above 7.5°C were not made, we have evidence (unpublished) that diapause development takes place and proceeds faster at temperatures above those studied here. A cohort of pupae, that pupated at 10°C at about the same time as the pupae used in the 4-temperature experiment (Fig. 1), was left at 10°C for two months and then transferred to 20°C. They developed to adults in an average of 30.5 days and approximately 47% of the pupae were apparently in diapause when transferred. By comparison, after two months storage at 7.5°C, the mean development time at 20°C was 33.1 days and approximately 80% of the pupae were in diapause. When other cohorts that pupated at 10°C (and therefore were presumed to be 100% in diapause) were placed directly at 20 and 15°C, they developed to adults with mean development times of about 40 and 46 days, respectively. These development times are about double the time expected at those temperatures for non-diapause pupae (Stevenson 1981), but less than the time required for non-diapause pupae to develop at 10°C. Therefore, the combined processes of diapause development and non-diapause development took less time at 15 and 20°C than the single process of non-diapause development at 10°C.

Knowledge of the response of diapause pupae to low temperatures can be used to advantage in management of the supply of carrot rust fly in laboratory research. This method would be

particularly useful if the researcher has access to a heavy field infestation of the pest, and quantities of diapause pupae, or larvae to pupate under diapause-inducing conditions, can be obtained and placed in storage. Our results show that 1°C would be the best of the temperatures studied for this purpose. Although diapause development was more rapid at 5 and 7.5°C, the occurrence of non-diapause development, higher pupal mortality, and greater variability meant that less effective control of numbers of adults and timing of emergence would be achieved. There was no evident advantage to the use of -2°C.

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(Received 3 June 1994; accepted 12 September 1994)

CORRIGENDA: CLASSIFICATION, RECONSTRUCTED PHYLOGENY AND GEOGRAPHICAL HISTORY OF THE NEW WORLD SPECIES OF *COPTODERA* DEJEAN (COLEOPTERA: CARABIDAE: LEBIINI)

D. SHPELEY and G.E. BALL
Department of Entomology, University of Alberta, Edmonton, AB Canada T6G 2E3

Corrigenda for paper published in the Proceedings of the Entomological Society of Ontario, Volume 124: 1-182 (1993).

p. 3 Abstract, second paragraph, line 6
México, Colima *should read* México, Jalisco

p. 29 couplet 3
3 (2') *should read* 3 (2)

p. 29 couplet 9
9 (8') *should read* 9 (7')

p. 29 couplet 12
12 (8') *should read* 12 (9')
12' [text]. . . .12 *should read* 12' [text] 13

p. 30 couplet 16
16 (14) *should read* 16 (15)

p. 31 couplet 29
29' of elytron present *should read* of elytron not present

p. 31 couplet 41
41 (37') *should read* 41 (38')
41 interval 4 of elytron *should read* interval 5 of elytron
41 interval 5 (Figs. 23B *should read* interval 4 (Figs. 23B

p. 32 couplet 41
41' interval 4 narrowly *should read* interval 5 narrowly
41' interval 5 (Fig. 23G) *should read* interval 4 (Fig. 23G)

p. 53 Type locality
Colima, México *should read* Jalisco, México

p. 128 Checklist, fourth last line
erwini, news *should read* erwini, new

1994 ANNUAL MEETING

The **Entomological Society of Ontario** is grateful for the support received for the **Annual General Meeting** held in St. Catharines on 23-25 September 1994 from: Agriculture and Agri-Food Canada, Pest Management Research Centre (Vineland), and Brock University.

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Note: Please provide figures to fit page sizes of the ***Proceedings****.*

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Volume 126 ***1995***

From the Editor,

When just over a year ago at the Society's meeting in St. Catharines I was asked to take over from Peter Kevan as editor of the Proceedings, I was both honoured and somewhat apprehensive. To follow in the footsteps of over a century of successful editors is a daunting task, and left me with the fear that I might screw up and let the Society down. But now, as Volume 126 'hits the newsstand', I have regained my confidence. I promise that I will do my best to continue to provide our membership and the scientific world at large with a well edited journal, full of interesting information, opinions and news.

I have availed myself of the editor's prerogative to make some changes in the editorial policy of the Proceedings. The reader will notice that the first article is a kind of 'forum' or 'opinion' addressing a major new development related to entomology written for a broad audience. This year's introductory paper is by Dr. Virginia Walker and co-workers of Queen's University. The authors describe their efforts to transfer antifreeze protein genes from fish to fruitfly, and ask some very challenging questions about two rapidly expanding branches of science that will affect entomology in the future: molecular biology and biotechnology. I intend to continue with this policy in future issues, by focussing on other trend setting developments in entomology. The other change is the inclusion of a couple of reviews of books that are either authored by Ontario entomologists and/or on the subject of Ontario entomology. Again, I hope to make this an ongoing component of the Proceedings.

A few administrative changes are also in the wind. The most important is that starting next year we will welcome manuscripts in French with English abstracts. Other changes are incorporated in the 'Instructions to Authors'.

The Society's Governing Board decided at its most recent meeting that next year's volume is going to be a 'festschrift' to honour Don Wallace who was a member of our society for many years until his recent death. Since Don was one of Canada's foremost forest entomologists, the 1996 Volume (No. 127) will be dedicated to forest entomology in its broadest sense: management, taxonomy, pollination ecology, overwintering physiology; anything goes! Let me urge you to start writing as soon as possible, and submit your manuscripts for the Don Wallace memorial volume of the Proceedings.

Above all, I want to stress that the editor and associate editors can only take credit for a small part of the success of a journal; the authors and the reviewers primarily determine the quality of a journal. The Proceedings are no exception. I want to thank all those who contributed to this volume for their high professional standards. This gives me confidence for the future.

Dolf Harmsen

THE TRANSFER OF FISH ANTIFREEZE GENES TO *DROSOPHILA*: A MODEL FOR THE GENERATION OF TRANSGENIC BENEFICIAL INSECTS

VIRGINIA K. WALKER[1], DERRICK E. RANCOURT[2] and BERNARD P. DUNCKER[3]

There are many reasons why molecular geneticists are interested in the transfer of genes from one organism to another, but a prime motivation is to confer additional, advantageous qualities to agricultural plants and animals. For the molecular entomologist, the investigation and application of gene transfer techniques (Walker 1989; Handler and O'Brochta 1991) offers the prospect of genetically engineering insects either for pest control, or to extend the range and attributes of beneficial species.

The *Drosophila* model

The ubiquitous fruit fly, *Drosophila melanogaster*, offers many advantages as a transgenic model system and therefore is an excellent organism for the experimental optimization of the expression of foreign genes. In *D. melanogaster*, the discovery of a "jumping genes" or transposable elements in wild populations has led to a reliable method of germ line transformation (Spradling 1986). Engineered plasmids containing transposable P-element sequences can be microinjected into pre-syncytial embryos. Typically, about 7% of the embryos survive to fertile adults and can act as founders of transformed lines (Spradling 1986). The fruit fly's short generation time (10 days), along with its well established genetics, make it easy to set up transgenic stocks. Although the introduced DNA could come from any source, it must contain a host-recognizable promoter and regulatory DNA in order to be transcribed. Genes from closely related *Drosophila* species are expressed (Bray and Hirsch 1986; Fisher and Maniatis 1986) and, remarkably, chorion and silk protein genes from the moth, *Bombyx mori*, have been transcribed in *Drosophila* ovarian follicles and larval salivary glands, respectively (Mitsialis *et al.* 1987; Bello and Couble 1990; Spoerel *et al.* 1993; Fenerjian and Kafatos 1994). Successful expression of DNA from other species (heterologous genes), however, is unlikely unless the particular promoter is unusually conserved, such as that of the heat shock 70 protein gene (*hsp70*) (Miller *et al.* 1987) or a metallothionein gene (Kovach *et al.* 1992), a long terminal repeat from a repetitive DNA element (e.g. copia: Tamura *et al.* 1990; Mathi *et al.* 1991) or a constitutively expressed actin gene (e.g. actin 5C: Atkinson and O'Brochta 1992). In contrast to the transcription seen with such constructs, no heterologous transcripts were detected in *Drosophila* lines containing coding regions and 2.5 kb of upstream sequence from the vitellogenin B gene from the African migratory locust, *Locusta migratoria* (Wyatt *et al.* 1986), nor was mRNA produced from a fish antifreeze protein gene with 0.5 kb of flanking regulatory DNA (Rancourt *et al.* 1987). In addition, there was no expression of an integrated yeast suppressor tRNA gene in transgenic flies (Molnar *et al.* 1988).

In order to force the expression of any gene, including those derived from other, perhaps evolutionarily distant organisms, one need only to appropriately join the coding region of the gene with regulatory DNA from *D. melanogaster*. This strategy of producing a chimaeric gene,

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regulated by a host-compatible promoter, can confer a new phenotype to the host insect. The prospect of transferring a resistance phenotype is particularly attractive. In the future, transgenic beneficial insects could be made more resistant to insecticides, the environmental extremes of heat, cold or desiccation, heavy metal pollution or oxidative stress. The use of transgenic beneficial insects, of course, should not encourage the use of environmentally irresponsible pest control practices, but would simply be an additional tool for the practitioners of integrated pest management (Hoy 1992, 1993). The lessons learned from the challenges posed by transgenic experiments, especially in the convenient *Drosophila* model, are necessary if we hope to eventually confer unique and useful properties to a variety of beneficial species.

Antifreeze protein genes

For the past decade we have been exploring the possibility that limited frost resistance can be conferred to insects by the controlled transfer and expression of antifreeze protein genes (AFPs). These proteins have been extensively studied in fish and can be divided into four different classes. Despite their structural differences, they all appear to act in a similar fashion, conferring freeze protection to their hosts by interacting with and inhibiting the growth of ice crystals within the serum (DeVries 1983). AFP activity assays include measurements of the difference between the melting point and the lowered freezing point of solutions containing AFP, termed thermal hysteresis. In addition, AFP activity can be assessed by the altered morphology of microscopic ice crystals; the presence of fish AFP inhibits ice growth in some directions and results in hexagonal bipyramid crystals rather than round, flat ice formation.

Difficulties with Transgenic Type I AFP Flies

Antifreeze glycoproteins (AFGPs) from Arctic and Antarctic fish vary greatly in size (2.6-33 kDa) and are heavily glycosylated with disaccharides (DeVries and Wohlschlag 1969; Osuga and Feeney 1978). The addition of sugar groups to proteins in foreign eukaryotic hosts is not always accurate and thus AFGPs are less attractive candidates for gene transfer. In contrast, Type I AFPs from flounders and sculpins are small (3 kDa), non-glycosylated, alanine-rich proteins. When the coding sequence from the winter flounder AFP was joined to the *D. melanogaster hsp70* promoter and used to transform *Drosophila* embryos (Rancourt *et al.* 1987), AFP mRNA was detected in transformed flies which had been heat shocked (37°C). AFP was detected immunologically in the hemolymph, showing that the heterologous protein was recognized by the *Drosophila* secretory protein system. However, there was insufficient accumulation of the foreign protein to result in measurable thermal hysteresis (Table I). Even when several of the separate transgenic fly lines were used in genetic crosses to generate flies with multiple copies of the *hsp70*/AFP gene there was still not enough AFP to result in thermal hysteresis (Peters *et al.* 1993). Assuming that the transiently expressed *hsp70* promoter was responsible for the low levels of AFP production, the *hsp70* sequence in the fusion gene construct was exchanged for the developmentally regulated, female specific *D. melanogaster* yolk protein 1 (*yp1*) promoter. This was chosen because it is not only a powerful promoter, but the use of inducible or sex-specific regulatory DNA sequences to drive heterologous coding regions is convenient since it allows the recovery of transformants independently (in this case, in males) of any lethal effect which may be associated with the expression of the foreign gene. Disappointingly, despite the presence of AFP mRNA in female transgenics, no AFP could be detected in their hemolymph (Rancourt *et al.* 1987; Table I). Type I AFP genes may present a special challenge to the insect's translational system since they are alanine-rich and there is a bias in the coding region such that there is a frequent reiteration of the GCC alanine codon. Flounder cope with the translation of this biased mRNA by the seasonal

TABLE I. A summary of antifreeze protein (AFP) expression in *Drosophila* adults transformed with different plasmid constructions.

Construct (promoter/gene)[1]	Conditions/Sex	Copy #	mRNA	AFP	Thermal hysteresis[2]
hsp70/Type I AFP	22°C	1-6	-	-	none
	37°C	1-6	+	+	none
yp1/Type I AFP	♂	1-2	-	-	none
	♀	1-2	+	-	none
yp1/Type II AFP	♂	2	-	-	none
	♀	2	++	++	0.13°C-0.16°C
yp1,2/Type III AFP	♂	1-2	-	-	none
	♀	1-2	++	++	0.14°C-0.20°C
yp1,2/Type III AFP/*yp1* 3'AFP	♂	1-2	-	-	none
	♀	1-2	++	++	0.12°C-0.35°C
yp1,2/Type III AFP/*yp1* 3'AFP	♂	4-8	-	-	none
	♀	4-8	++	++	0.29°C-0.43°C

[1] The fish from which the AFP genes were obtained were winter flounder (Type I), sea raven (Type II) and wolffish (Type III). The heatshock 70 (*hsp70*), yolk protein 1 (*yp1*) or the yolk protein 1 and 2 intergenic region (*yp1,2*) promoters were used to force the expression of the AFP genes in *Drosophila*.

[2] Mean values from individual transgenic lines. The chromosomal position of the transgene can influence its transcriptional activity (position effect) and result in some variation in AFP levels.

increase of a $tRNA^{Ala}$ (Pickett *et al.* 1983) but presumably, transgenic *Drosophila* do not have sufficient reserves of this charged tRNA to cope with the translation of an abundant *yp1*/AFP transcript as well as the other endogenous messages (Rancourt *et al.* 1992). Some AFP was produced when the gene was under the control of the *hsp70* promoter probably because genes with *hsp* regulatory elements are preferentially transcribed and translated during heat stress. As well as this barrier to heterologous protein accumulation, Type I AFP also has other "difficult" properties. In flounder, the proform of the AFP is quickly converted to a somewhat more active mature form in the serum. This does not occur in transgenic flies (Peters *et al.* 1993). In addition, the secondary structure of the flounder AFP seems to be temperature sensitive, so that at -1°C the protein is 85% α-helical, but at 25°C, the normal *Drosophila* rearing temperature, this value drops to 47% (Ananthanarayanan and Hew 1977). The small amount of AFP found in the hemolymph of *hsp70*/AFP transgenic *Drosophila* persists longer if the flies are kept at a temperature (10°C) closer to that of the fish habitat (Duncker *et al.* submitted). The decrease in AFP accumulation at 25°C appears to be at least partially due to a temperature-dependent persistence in AFP mRNA; message from transgenic flies reared at 10°C was more stable than in flies at the normal rearing temperature (Duncker *et al.* submitted). Thus, to enhance the success of any effort to transfer foreign genes to insects, it is important to select an appropriate host promoter, know something

of the codon bias of the coding sequence and of the host insect and, very importantly, to investigate the expression and regulation of the chosen gene in the donor organism.

Success with Transgenic Type II AFP Flies

In contrast to Type I AFP genes, Type II AFPs sequences show no significant codon bias. These encode globular, cysteine-rich proteins of 14-24 kDa which are found in sea raven, herring and smelt (Davies and Hew 1990). Chimaeric genes were made by the joining of the *Drosophila yp1* promoter with a genetically engineered sea raven AFP DNA. Transgenic females produced both Type II AFP mRNA and protein (Duncker *et al.* 1995b; Table I). In this case sufficient AFP was produced so that when hemolymph was assayed for AFP activity, ice crystals grown at low temperatures formed microscopic hexagonal bipyramids (Fig. 1) and there was a detectable level of thermal hysteresis. In addition, microscopic examination of ice recrystallization in hemolymph samples rapidly frozen to -133°C formed smaller ice crystals at 10°C, -3°C and at melting, suggesting that tissue damage might be less when frozen, transgenic lines are thawed. Type II AFP is produced in fish as a preproprotein and, as was the case with the Type I AFP, *Drosophila* fat bodies appropriately secreted the proprotein. Again, however, the pro sequence was not removed from the protein in the hemolymph or in insect cells in culture (Duncker *et al.* 1994, 1995b). Thus the proteinase activity responsible for the hydrolysis to mature AFP in sea raven serum is absent in *Drosophila* hemolymph.

High Thermal Hysteresis in Transgenic Type III AFP Flies

To further demonstrate that the selection of an appropriate heterologous gene is crucial to the success of any transgenic production, and to improve the level of heterologous protein production, gene fusions were made using a third candidate, the Type III AFP gene from wolffish. These AFPs, which are characteristic of eel pouts, are globular 6 kDa proteins with a β-sheet structure and have no particular amino acid bias (Sönnichsen *et al.* 1993). The *Drosophila* yolk protein promoter region was again selected to force the expression of the Type III gene. In these experiments, the entire 1 kb region which directs transcription, in opposite directions, of the yolk protein 1 and 2 genes (*yp1/2* 5' sequence) was used as the promoter DNA. Two copies of the AFP genes could then be divergently transcribed from this single intergenic regulatory region (Rancourt *et al.* 1990). This mimics the situation in the wolffish where most of the AFP genes are organized in divergent transcriptional orientation (Scott *et al.* 1988). The ligation between the yolk protein and AFP coding regions was made by an in-frame fusion between the sequence encoding the yolk protein secretory signal peptide and the AFP signal peptide near the end of the hydrophobic core. These experiments were successful and transformed adult females from individual lines showed thermal hysteresis readings of 0.14-0.20°C (Table I).

Other constructs containing sequences which could possibly result in greater AFP accumulation were also investigated. Both the *yp* and Type III AFP coding regions are interrupted by intervening sequences. These intervening DNA sequences, or introns, appear to be important for the accumulation of transgene RNA since the deletion of the wolffish intron in the construct resulted in a 2-11 fold decrease in the AFP mRNA relative to a control gene (Duncker *et al.* unpublished). When the deleted intron was replaced by the *yp1* intron, levels of AFP transcripts were restored to pre-deletion levels. Thus the presence of an intron *per se* appears to be important to maximize transgenic mRNA accumulation. When the 3' untranslated region of the *yp1* gene was substituted for that of the AFP gene in the *yp1/2*AFP construct, one of the derived transgenic lines showed the highest hemolymph thermal hysteresis value (0.35°C) obtained in a single insert stock (Rancourt *et al.* 1990; Table I). After individual lines containing this chimaeric gene were

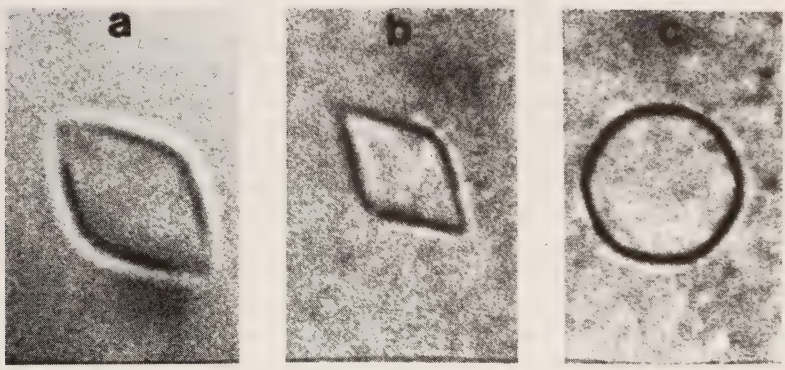

FIGURE 1. Ice crystal morphology. The samples analysed were sea raven Type II AFP purified from fish serum (a), hemolymph from female *Drosophila* obtained from a transgenic line containing the sea raven AFP coding sequences joined to a *Drosophila* yolk protein promoter (b) and hemolymph from female *Drosophila* obtained from the untransformed, host strain (c). Magnification of the ice crystals was 700-fold.

crossed so that transgenic flies with additional copies of the AFP coding regions were generated, thermal hysteresis levels went up to levels approaching those found in some overwintering fish (Duncker *et al.* unpublished). In order to increase the transgene copy number to the 30-150 gene copies found in fish, however, conventional genetic crosses are not practical. A promising alternative would be to cross these lines to flies containing a functional copy of the P element vector's transposase (Robertson *et al.* 1988; Meister and Grigliatti 1993) to mobilize the integrated transgenes and catalyse their insertion at numerous genomic sites.

Disappointingly, when a single insert line was tested for resistance to cold exposure at 0°C and at -7°C, the survival of the AFP-containing flies was no better than their control siblings (Duncker *et al.* 1995a). At these temperatures the flies do not freeze and the studies were primarily a test to determine the role of AFPs in membrane protection (Rubinsky *et al.* 1990; Rubinsky *et al.* 1991). One must conclude that some other consequence of cold exposure had a greater influence on the insects' survival than from the proposed AFP-mediated membrane protection.

Transformation of other insects

Although the principles demonstrated in the efforts to transform *Drosophila* embryos with fish AFP genes are important for attempts to transfer resistance phenotypes to beneficial insects, the P element vectors used in this research do not mediate transformation of other genera. There is an active search for methods to transform other insects including the investigation of various

transposable elements as mediators of gene integration, such as mariner (Robertson 1993; Lidholm *et al.* 1993), hobo (O'Brochta *et al.* 1994) and P elements (Miller *et al.* 1987), as well as the use of an assortment of viruses (e.g. Kim *et al.* 1994), the direct injection of DNA into embryos or adult females (Miller *et al.* 1987; Grane *et al.* 1988; Presnail and Hoy 1995) or the treatment of insect semen with DNA (Atkinson *et al.* 1991). Apart from *Drosophila*, insects considered as useful subjects for this genic manipulation, and for which some success or efforts to transform have already been reported, include the beneficial species: the parasitic wasp, *Cardiochiles diaphaniae* (Presnail and Hoy 1995), the honey bee, *Apis mellifera* (Atkinson *et al.* 1991) and the silk moth, *Bombyx mori* (Tamura *et al.* 1990). Most impressive are the experiments of Hoy and her colleagues with arthropods. A reporter gene composed of the *Drosophila hsp70* promoter joined to bacterial β-galactosidase DNA was microinjected into adult female predatory mites in the vicinity of the ovaries. The introduced DNA was taken up into the eggs and appears to be integrated into the genome in at least one line (Presnail and Hoy 1994). Additional lines were obtained when the marker DNA and a fragment from the transposable element, mariner, was coinjected and there is some evidence that integration may have occurred by targeted transposition into the mite endogenous mariner sequences (Jeyaprakash and Hoy 1995).

Techniques for the transformation of pest insects are also being sought for use in the eventual control of disease transmission and agricultural losses. Species of interest for transformation include the malarial *Anopheles* vectors (Miller *et al.* 1987), viral *Aedes* vectors (Grane *et al.* 1988; Crampton *et al.* 1990; Morris *et al.* 1991), the Chagas disease vector, *Rhodnius*, through a bacterial symbiont (Beard *et al.* 1992), the tsetse fly, *Glossina morsitans,* through a bacterial symbiont (Beard *et al.* 1993), the housefly *Musca domestica* (Atkinson *et al.* 1993), the Australian sheep blowfly, *Lucilia cuprina* (Atkinson and O'Brochta 1992) and the Queensland fruitfly, *Bactrocera tryoni* (O'Brochta *et al.* 1994) to name but a few.

Resistance genes for transfer

Candidate genes for transfer to beneficial insects which might make them more resistant to various environmental stresses include fish AFPs or perhaps the more active insect AFPs (Rahavard, Davies and Walker unpublished), the desiccation stress protein gene from *Tenebrio* (Graham *et al.* 1995), and the control genes or elements governing thermotolerance in tropical insects (Whyard *et al.* 1987; Gehring and Wehner 1995). Interest in increasing the insect lifespan, as well as enhancing fertility has prompted the transfer of either bovine or fly superoxide dismutase genes (Orr and Sohal 1993; Reveillaud *et al.* 1994). When this gene was transferred along with a catalase gene, the life span of the transgenics was extended by as much as one third relative to controls (Orr and Sohal 1994). Flies with additional copies of the metallothionein gene show increased resistance to heavy metals (Maroni *et al.* 1987) and transgenic *Drosophila* carrying a detoxification gene showed significant resistance to chemical toxins compared to nontransgenic controls (Komori *et al.* 1993). Among the list of "resistance genes" those which may be of most interest are those conferring an insecticide resistant phenotype. They offer the potential of useful selective markers in the identification of transgenic individuals as well as having possible use in beneficial insects used in pest management strategies. Genes which confer organophosphate insecticide resistance have been used to transform *Drosophila* (Phillips *et al.* 1990; Fournier *et al.* 1992) and there are reports of transfer to a parasitic wasp (Presnail and Hoy 1995) and a mosquito (Yardley *et al.* 1995).

Cautions and conclusions

The transfer of any new phenotype to even a beneficial insect requires that reasonable precautions should be established. Particular care must be taken to avoid releasing insects that have been transformed with an active transposable element or viral vector and which could provide a selective advantage to their host. The fish AFP gene transfer to *Drosophila* was undertaken using host insects that were genetically manipulated so that they were unable to fly. They included the dominant mutations, Wrinkled (*W*), which have wavy, non-functional wings or Intermediary flight muscle 3 on the third chromosome (*Ifm(3)3*) which are unable to jump or fly (Rancourt *et al.* 1991; Duncker *et al.* 1993). Even if the transformed flies "walked" out of the lab, none of their progeny from potential crosses outside the laboratory would be able to fly because heterozygotes also have the flightless phenotype. For other insects with limited genetic markers, and particularly for pest species, suitable vigilance to prevent escape should be practised if a selectively favoured transformed strain is obtained. For beneficial insects it is important to restrict the introduced gene to that species. We do not yet understand the mechanism or frequency of horizontal gene transfer, but it would be wise to ensure that if integration was achieved by a transposable element, a potentially integrating copy of the transposase gene was not included in the introduced DNA, in order to limit the spread of the gene to only the progeny of the released insects. Hoy and her colleagues have avoided some of this uncertainty by maternal microinjection of arthropods rather than the use of intact transposable element vectors (Presnail and Hoy 1994). In addition, Marjorie Hoy has developed criteria for the release of molecular genetically manipulated arthropods and devoted considerable reflection to the issues raised by this technology and the risks involved (Hoy 1992, 1993).

The transfer and expression of a foreign gene in an insect is obviously not a trivial problem. The lessons learned from the efforts to transfer AFP genes to flies have demonstrated several beginning steps, including the prudent selection of the target gene, the choice of promoter, the inclusion of intronic and other regulatory sequences, the consideration of copy number, the manipulation of the host so that it is effectively contained and an appreciation of the ecology of both the gene donor and the recipient. It is hoped that these investigations, as well as the admonition for a cautious approach, will prove valuable for future studies on the transfer of a resistance phenotype by the genetic transformation of insects.

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BUTTERFLY CONSERVATION PROGRAMS MUST BE BASED ON APPROPRIATE ECOLOGICAL INFORMATION

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Butterflies are highly visible insects, and serious population declines have been recognized in many regions of the world. Losses in diversity and numbers are generally attributed to anthropogenic effects, particularly loss of habitat through major changes in land use. Many nations are now supporting conservation efforts, but failures are frequent. These can result simply from the impact of adverse density independent factors on small populations in sub-optimal habitats. Grassland and woodland butterflies are often adapted to various intermediate states of vegetational climax, especially in temperate zones. This means that reserves have to be actively managed to maintain specific abiotic and biotic conditions, which may include specific grazing effects by vertebrates and associated ant species in the case of some lycaenids. Adult food resources are as vital as adequate supply of larval foodplant. Environmental factors need to be assessed on a case by case basis. Active research programs are essential, to provide pertinent and relevant information to managers on the ecological requirements of endangered habitats and species.

Introduction

There are many reasons why we must develop sound conservation strategies to protect all groups of invertebrate animals as discussed by Pyle (1981), Pyle *et al.* (1981), New (1991) and the Canadian Nature Federation (1993). Few butterfly species are agricultural or forestry pests of any magnitude (Kudrna 1986). Some, along with moths, may be significant pollinators of field and horticultural crops, orchards, wild-flowers and native shrubs and, in the tropics, a number of flowering trees. Worth noting however, are the contrary observations of Wiklund *et al.* (1979) and Courtney *et al.* (1982), who concluded that many butterflies, because of the length of the proboscis, functioned as 'nectar thieves', transferring only minimal amounts of pollen for fertilization. Most butterfly larvae feed on indigenous plants or rough grasses, and some eat introduced 'weed species'. Such consumption exerts a measure of control on plant growth and proliferation and in the case of larvae of *Vanessa* spp. feeding on nettles and thistles, there is direct minor benefit to human agriculture.

How We Lose Species - Remorseless Habitat Degradation

The composition of the insect fauna of a region is partly a function of its paleohistory (Dennis 1977, 1992b). Beyond that, limits to animal distributions often can be ascribed to latitude and

altitude effects (Dennis 1977, 1992a; Matsakis 1986). For most temperate zone butterfly species, successful thermoregulation is the key to survival (Douglas 1986; Shreeve 1992a; Warren 1993; Pollard and Yates 1993) and this may be measured by the number of hours of unshaded sunshine per day available during critical growth periods in the life cycle (Kudrna 1993).

The literature on ecology and conservation of butterflies has grown considerably in the last decade but the general picture is not reassuring. Diversity of butterfly communities has declined in most regions where surveys have been conducted (Ehrlich and Ehrlich 1981; Ehrlich 1984), and in parts of Europe losses have been documented for at least a hundred years (Conquest 1897; Frohawk 1925; Ford 1945). The Netherlands has lost almost a quarter of its butterfly fauna. Most losses can be attributed to anthropogenic activities (Kudrna 1986). Reductions in range and extinctions of local populations have accelerated since the 1960s (Thomas 1984), largely as a result of agricultural policies directed to maximization of economic efficiency, with concomitant changes in almost all traditional farming methods (Blab and Kudrna 1982; Thomas 1984; Feltwell 1986; British Butterfly Conservation Society 1992). Barbour (1986) and Heath (1981) suggested that air pollution might be a factor also, but the evidence is still ambiguous (Dennis 1992a). The reduction of habitats and diversity in tropical rain forests has justifiably received much attention in recent years (Myers 1986). Nevertheless, the losses of temperate zone native grassland, heath and wetland have been proportionally much greater, brought about by chemical improvement and drainage, systematic hedgerow removal, regular spraying of rural road verges, conversion of marginal grazing land to tree plantations, and continual urban expansion. It is not surprising that a large proportion of endangered butterflies are endemic to these habitats (Stolzenburg 1992; British Butterfly Conservation Society 1992).

The will to conserve a habitat or species is the necessary starting point, but to succeed in conservation this must be supported by hard work, funding and appropriate information about the habitat and the ecology and life cycle of the species involved. Unfortunately, the stimulus for most conservation action is belated recognition of a crisis (Pyle 1981; Thomas 1984). Naturalists have observed for decades that butterflies can exhibit large variation in population size, from brood to brood and year to year, even under normal conditions. Consequently, it may take 5-10 years before a population collapse is recognized (Farrell 1975). Studies often begin only at this stage, and the cause of reductions or extinctions may remain forever speculative.

Sometimes butterfly reintroductions or natural recolonizations are successful and sustained (Thomas 1992). In such cases, we can conclude that a change in the habitat was not the original problem. Local weather records may indicate that stochastic climatic events might have been responsible, overwhelming the colony's capacity to replenish itself and leading to rapid extinction (Shapiro 1979; Ehrlich *et al.* 1980; Murphy and Ehrlich 1980; Dempster 1993). Drought is a common factor in such events (Ehrlich 1984). The second attempt to reintroduce Large Copper *Lycaena dispar* butterflies at Woodwalton Fen, England, failed as a result of one major flood (Duffey 1977; Thomas 1984). Local extinctions are often facilitated by habitat fragmentation, and the impact of density-independent factors is likely to be least when butterfly colonies are numerous and dispersed but within the limit of the average mobility of the species.

Local extinctions will still occur in such a mosaic (Shapiro 1979), but suitable habitat is eventually recolonized. 'Permanent' extinctions (i.e. on the human time scale) are more likely when colonies are isolated and near the limits of their normal range. Such restricted populations experience a degree of inbreeding; the impact depends partly on the size of the colony, but is minimized if matings are more or less random. Loss of genetic diversity will occur if such populations are periodically reduced to low numbers. Drought or flood can cause significant

increases in mortality, and subsequent periods of cold or sunless weather may greatly diminish the chances of population recovery, regardless of the level of genetic diversity in the colony.

Variation between and within communities in habitats of similar structure is not necessarily obvious; recently Housego and Gormally (1993) and Steel and Mills (1988), found significant differences in diversity and density of invertebrates in hazel coppices at varying age of regrowth in Britain. On the other hand, Hill and Stork (1990) reported that in birch and sweet chestnut woodlots subjected to similar management, densities and biomass of invertebrates showed virtually no differences.

A difficult question for butterfly conservation managers is "why are some butterflies always rare"? Pollard and Yates (1993) noted that some species are often under-counted by transect surveys. Possible causes include concentration of butterflies in local colonies (e.g. European *Melanargia* spp.) that are missed by the transects, by species being largely restricted to woodland canopy and out of sight of observers (e.g. European *Apatura iris*, and *Quercusia quercus*), low sightability because of cryptic coloration, behaviour or flight in shaded margins (e.g. some New World *Megisto*, *Euptychia* and *Pierella* species), or real rarity as a function of small population size. Determining whether any taxon is truly rare can be difficult (Rabinowitz *et al.* 1986; Hubbell and Foster 1986). Some butterflies, such as the large, strong-flying papilionids, nymphalids and hesperiids of the tropics, can have large geographical ranges as species and large individual "home ranges". In this case, low population density does not equate to actual rarity.

Long-term field studies are the only way to solve many of these puzzles. "Rare" can be just a reflection of "surveys not done in the right habitat", "surveys not done in the right months", sometimes "surveys not done in the right years". Similarly, it may take several years to determine if a population is sustained only by annual immigrants. A summer brood may emerge regularly and a proportion of an autumn brood might overwinter in years when weather or autumn feeding conditions were favourable. Do we classify such a population as "residential" if it has hung on for several successive years?

When distributions are clearly localized and low population density is not balanced by high mobility, we may safely categorize species as "rare", and perhaps "vulnerable". If the life history of a species is poorly known, then research should be given a high priority. We should not assume automatically that rarity or recognized declines always reflect an underlying anthropogenic effect. Some populations may be held at low densities by resource limitation, predators, parasites or diseases. Dempster (1967, 1971, 1984) and Baker (1970) have reviewed the natural pathogens, parasites, parasitoids and both vertebrate and invertebrate predators of butterflies. Parasitic outbreaks may kill hosts, but often just slow growth and development, so the butterflies survive to reproduce. The attacks of parasitoids are usually fatal, but also strongly dependent on host density. Morrison and Strong (1980) and Strong (1984) argued that parasitoids and predators play an important role in keeping populations of phytophagous insects at low densities on *Heliconia* plants. Dempster (1984), however, doubted that existing data support a case for parasitoids exerting a strong control on population size of butterflies. He noted that interdependence between host and parasitoid populations can induce oscillations in population size in alternate generations, sometimes with delayed density dependence (*cf.* Ito *et al.* 1960). Complex or erratic oscillations are also common in such data sets, however, because the host population is being attacked by more than one species of parasitoid. Other confounding environmental influences on population size and annual mortality rates are often involved.

Conservation Strategies - What Works and What Doesn't

Butterflies occupy a range of global habitats from deeply shaded tropical forest to arctic and high altitude tundra, yet particular demes can exhibit puzzling, and apparently non-adaptive variations in food plant selection and other behaviour (Ehrlich 1984). One of the best known examples is the English population of *Papilio machaon*, restricted to one larval foodplant and shrinking fenland (Dempster 1984) while its compatriots on the mainland of Europe utilize a wide range of foodplants, are a common sight in woodland margins and meadows and seem to demonstrate a particular attachment to Roman and Greek archaeological ruins. Similarly, although we can explain why *Artogeia* (*Pieris*) *rapae* became a pest when it began to feed on our monocultural cruciferous crops, we do not understand why its close relative *A. napi* did not (Yamamoto and Ohtani 1979; Ehrlich 1984). A population will use a suboptimal foodplant when there is no alternative (Shapiro and Masuda 1980). Courtney (1984) suggested that this behaviour is a function of the life span of the gravid female and the potential numbers of hostplants she might encounter in that period; in evolutionary terms it is probably more advantageous for her to oviposit on suboptimal foodplants than die with many eggs still unlaid. It is much less clear why some butterflies continue to use suboptimal foodplants when more suitable ones become available (Ehrlich 1984).

The best butterfly conservation strategy for agencies would seem to be pre-emptive protection or purchase of relatively large tracts of each type of habitat in each major geographical region of the country, rather than to focus on trying to save highly endangered, isolated colonies in sub-optimal habitat. Of course this is much easier said than done, because so much land in any developed country is already in private hands and often ecologically modified. Nor is such a strategy always successful, unless those lands are managed and maintained for particular butterfly species. While Great Britain has one of the best records for preservation and re-establishment of rare butterfly species, it is still far from perfect. Many of the protected sites on which colonies of endangered species survive were originally selected with conservation of rare birds or mammals as the primary objective, or because they represented a good microcosm of a particular county landscape.

One of the problems of conserving such habitats is that the temperate grassland flora evolved in concert with the impacts of natural fires and grazing and browsing mammals. Furthermore, different species of phytophagous vertebrates have markedly different impacts on grassland structure and composition (Oates 1993). Removal or reduction of specific grazing pressures initiates changes in the composition of the vegetation, which in northern temperate grasslands typically takes the form of fairly rapid transition to scrubland. This may favour some of the hairstreak butterflies, but is to the detriment of a number of the blues. Clearly, it is not enough just to protect habitat from development, or fence it to keep specific browsers or grazers either in or out. Active management is essential in almost all situations.

Thomas (1984) documented what he called the "appalling" history of extinctions of rare butterfly colonies on British nature reserves. There were several reasons for this, the primary one being past failure to realize that some butterflies thrive not just in particular habitats, but also at intermediate stages of vegetational climax. In Great Britain the Heath Fritillary *Mellicta athalia* survives only where early successional woodland is maintained (Warren 1987a,b; Warren *et al.* 1984). In the absence of grazing animals, which are often excluded from reserves, some of the short turf-grass skippers and blue butterflies invariably decline (Thomas 1984). Throughout the temperate zones of both hemispheres many butterfly species are adapted to early to mid-transitional seres within a given biome. Suitable conditions may exist for only a few years at any one site,

so that relatively large areas of contiguous habitat must be preserved to facilitate continuous recolonizations. In Texas, the Dwarf Yellow *Nathalis iole* thrives on small species of weedy Asteraceae that colonize thinly-grassed stony slopes and eroded flood plain areas. Once the taller perennial grasses begin to predominate, *N. iole* often becomes much less abundant.

In Europe and temperate North America the combination of annual ploughing and chemical fertilization, rather than fallow rotations, and the removal of hedgerows to increase field size, have had disastrous effects on meadow butterfly populations. The destructive tide initiated by modern agricultural and forestry economics and the drive for maximization of short-term profit cannot be turned in the immediate future. In most developed nations we must look to managed reserves as the best hope for conserving woodland and grassland butterflies with localized distributions. A number of steps must be taken to set up a successful reserve. *First*, long-term commitments from governmental and private agencies are essential because maintenance of reserves is costly. *Second*, we require appropriate methodology to monitor population size over time and to provide indices of success or failure of various conservation approaches. *Third*, research programs must be sustained because the best way to improve management success is by trying various regimes and carrying out experiments supported by long-term data bases.

Commitment by Interested Agencies

The major organizations promoting insect conservation are the Xerxes Society in North America, the Societas Europea Lepidopterologica in continental Europe and the British Butterfly Conservation Society in the United Kingdom. Thomas (1984) noted that the BBCS was founded in 1968 and had 1800 members by 1981, but was "still too small to undertake major practical projects". However, in the last 15 years growth has been remarkably strong - BBCS now has over 9,000 members, 25 regional branches and some level of responsibility for about 900 managed sites throughout the U.K. It is also lobbying the British government to support the E.U. (European Union) "Habitat Directive", which, if passed in its full form, would require member states of Europe to protect threatened habitats. Internationally, influence is being exerted by the Lepidoptera Specialist Group of the Species Survival Committee of I.U.C.N. (International Union for the Conservation of Nature and Natural Resources), with headquarters in Gland, Switzerland. The I.U.C.N. has published a Red Book of threatened swallowtail butterflies of the world (Collins and Morris 1985) and, more recently, produced a global action plan specifically for species of this family (New and Collins 1991). New (1990) has also produced a directory of conservation projects on Lepidoptera.

Monitoring Populations

Popular articles and programs on ecosystem health have familarized the public with the concept of using 'key' species as indicators to monitor changes in populations, habitats and entire ecosystems. Kudrna (1986) and Wilcox *et al.* (1986) argued that butterflies had exceptional value as highly visible bio-indicators, and Hammond and McCorkle (1984) concluded that fritillary butterflies of the genus *Speyeria* (and their violaceous foodplants) were among the best indicator organisms by which the level of disturbance of native North American communities could be estimated.

Pollard (1977, 1979, 1991), Pollard and Yates (1993), Shreeve (1992b), Thomas (1983) and others, pioneered quantitative monitoring of butterfly populations in the United Kingdom, not only to assist the conservation of particular species, but also to provide possible indications of changes in habitats. It is not unreasonable to suspect that persistent reductions in numbers and diversity of one highly visible taxonomic group might be paralleled by similar declines in other, more cryptic groups of insects that are just as ecologically important. Such data are sadly lacking for most invertebrates in almost every part of the world. Obviously, if resources permit, the specific relationships and responses to change should be studied group by group. However, the general appeal of butterflies and their high visibility, coupled with the existence of good field guides for identification of species in most parts of the world, makes them more suitable for early warning monitoring than most other invertebrates. During periods of economic restraint it is valuable to have the services of volunteers in such survey projects. It is not too difficult or time-consuming to train science students, or even non-scientists, to correctly identify *en marche* a large proportion of the butterfly species they might encounter during field observations in North America and Europe. Far fewer amateur naturalists can identify specimens of other insect orders to species level in the field.

Future Research and Management Options

Kudrna (1986) commented that the biggest factor in successful conservation of endangered butterfly colonies was probably luck, because most circumstances are beyond the control of those in charge. He also argued that the failure to re-establish *Papilio machaon* at Wicken Fen in East Anglia (Dempster and Hall 1980) and to avert the extinction of the Large Blue *Maculinea arion* in its last stronghold in Britain (Thomas 1980) had the positive effect of encouraging research. There is no doubt that application of new information about the relationship of *M. arion* and its host ant (Thomas, J.A. 1993) was crucial in the recent successful re-establishment of the species in southwest England with stock from a continental population.

In the absence of research on ecological requirements and life cycles, the only interim measures that might slow declines in local butterfly populations are immediate protection of habitat, some attempt to rectify obvious changes in larval or adult food supply, and to reduce excessive shading in woodlands. In the long run, however, there is no substitute for the kinds of painstaking field and experimental work being done by the small groups of university, independent and governmental researchers in the United Kingdom, the United States, Japan, Australia and some of the European countries.

Too many governments have chosen the deceptively simple (and of course, relatively inexpensive) route of prohibiting collecting, transport and trade of specimens under the international C.I.T.E.S. (Convention on International Trade in Endangered Species) agreement. Such legislation often provides for large penalties, but is rarely supported by any significant, specialized policing effort. This is an attractive option for elected officials and government bureaucracies, because it gives the illusion of decisive remedial action with minimal budgetary pain. Worse, public concern wanes because a solution seems to have been found, and the efforts of good amateur entomologists are frequently discouraged by intricate permit processes required before they can collect and retain specimens. Meanwhile, the real culprits, habitat destruction and degradation, continue unabated (Kudrna 1986). Of course there is value in having legislation to protect against outright poaching of endangered species and the grosser excesses of commercial collecting from unique habitats (Daley 1995). Nevertheless, poorly framed regulations, especially

the kind of unnecessarily punitive prohibitions in force in Germany, cause more problems than they solve, especially in the absence of habitat protection. In this particular case, valuable research programs of professional conservation scientists were disrupted and even terminated (Kudrna 1986).

In the United States, the 1981 amendments to the Lacey Act have discouraged amateur research and survey efforts, while threatening technical violators, as well as actual poachers, with penalties of absurd severity (Heppner 1993). Furthermore, the absence of a coherent plan and insufficient government resources to properly implement the U.S. Endangered Species Act of 1973 has led to haphazard and often irrational decisions (Mann and Plummer 1992). Ill-chosen definitions and over-zealous application of this act have alienated landowners across the nation. An atmosphere of mutual distrust and suspicion has now made it almost impossible to contemplate the United States developing the kind of unique symbiosis of government agencies, trusts and landowners working together on habitat conservation that exists in Britain.

In Canada, the lack of mandate, infrastructure and basic understanding of the value of conserving insects and other invertebrates has been a matter of concern to biologists for many years. In Ontario, belated programs by the Ministry of Natural Resources failed to preserve the last remnant Canadian populations of the Karner Blue butterfly *Lycaeides melissa samuelis* and the Frosted Elfin *Incisalia irus*. Detailed studies of the ecological requirements of these species are still needed. Furthermore, many lepidopterists in the province remain disturbed by the action of the same department in reclassifying the West Virginia White *Artogeia (Pieris) virginiensis* from 'endangered' to 'rare' status (i.e. no longer protected). This decision was based on two seasons of surveys indicating that although still uncommon the species was more widespread than previously thought. There was no provision to recognize that it is sparsely distributed only in a small number of Transition Zone habitats, many of which are threatened with some degree of modification or outright development (see Hess 1990a,b, 1991a,b and Holmes *et al.* 1991). Within weeks of the de-listing, a developer completely destroyed one of its best habitats in southern Ontario.

One bright spot in the Canadian picture has been the initiation of the Biological Survey of Canada (Terrestrial Arthropods) by the Entomological Society of Canada in 1977, which has continued under the leadership of the Canadian Museum of Nature (1994) since 1980. The second is a new initiative of the Canadian Nature Federation (1993), specifically directed to conserve endangered cryptogamous plants and invertebrates in Canada.

Butterfly conservation has a long way to go and we can expect more extinctions as governments retrench and resources to deal with environmental problems are further reduced. Minimum requirements must include sustained habitat protection, supported by research on the optimal requirements of entire invertebrate communities. We still need information on the life cycles and habitat requirements of a large number of species in decline in many parts of the world.

The mobile cosmopolitan butterflies will probably be able to look after themselves, not only because they can cover considerable distances between preferred sites (Dempster 1989), but also because some species adapted to anthropogenic habitats centuries ago, including rough common grasslands, hedgerows, gardens and urban parks. Gaskin and Littler (1993), for example, recorded twice as many butterfly species in the town of Monemvassia in southeastern Greece than in the surrounding improved agricultural land.

Fortunately, even strongly colonial butterflies may not need huge tracts of protected land - 50 ha is often adequate for sustained survival (Thomas 1984). Under some circumstances small colonies can be preserved in less than optimal conditions by sustained management intervention, as in the case of two endangered Australian species, *Paralucia pyrodiscus lucida*, the Eltham

Copper, and *Hesperilla flavescens*, the Altona Skipper (New 1991), and the Large Copper butterfly, *Lycaena dispar* at Woodwalton Fen in eastern England (Duffey 1977). Nevertheless, such isolated populations are doomed sooner or later. Kudrna (1986) commented wryly that the Woodwalton population was more or less on an artifical life-support system.

We must protect and develop a matrix system of colonies (or meta-population) of threatened species (Thomas, C.D. 1993), never forgetting to leave or establish vital corridors between the habitat fragments if distances are more than a few hundreds of metres. Experience in Britain with species such as the highly colonial *Melanargia galathea* suggests that these corridors need not provide optimal habitat. As long as they offer suitable nectaring resources, they should facilitate enough movement of wandering adults to supply new recruits to periodically depleted colonies.

Appropriate nectar sources for adult butterflies are as critical as adequate provision of larval foodplants. The quantity and quality of nectar is unpredictable, varying with humidity levels, time of day, air temperature and the age of the flowers (Percival 1961; Corbet 1978; Shreeve 1992a) so a profusion of preferred flowering plants must be available throughout the season. Additionally, the shape and vegetation density of reserves for butterflies must be managed to suit particular species. Larger populations can be sustained in woodland habitat if an "edge effect" is enhanced by opening and maintaining rides and glades (see Lovejoy *et al.* 1986). The close-packed, circular woodlot model with minimum edge effect, most suited for songbirds (Wilson and Willis 1975; Wilcove *et al.* 1986) is not at all appropriate for most temperate zone butterflies.

Quantitative monitoring should be carried out regularly in colonies where crises might arise. We have to bear in mind that routine monitoring transect methods alone may not be sensitive enough to detect an impending crisis, because of the large statistical variance that usually attends periodic counts. There is probably no substitute for the experience of a field biologist familiar with a series of related sites over a number of years. Unfortunately, these are the people only too likely to be considered as expendable by government departments operating under the increasing fiscal pressures of the coming decade.

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REDUCED VULNERABILITY TO HYPERPARASITISM IN NONDIAPAUSE STRAINS OF *COTESIA MELANOSCELA* (RATZEBURG) (HYMENOPTERA: BRACONIDAE)

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The vulnerability to predation and hyperparasitism of an introduced European strain of *Cotesia melanoscela* (Ratzeburg) (Hymenoptera: Braconidae) and an Asian strain of the parasitoid with a different cocoon morphology and no diapause stage was compared in southern Ontario, Canada. The rates of predation and hyperparasitism were not related to cocoon morphology but were dependent on the length of time that cocoons were exposed to hyperparasitism in the field. The nondiapause characteristic of the Asian strain decreases its exposure time and hence reduces its vulnerability to hyperparasitism. Inundative release programs involving *Cotesia* spp. will be more effective using nondiapause strains of this parasitoid and by making releases as early as possible in the season to minimize their exposure to hyperparasitoids.

Introduction

Cotesia melanoscela (Ratzeburg) (Hymenoptera: Braconidae) is a primary parasitoid of the gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae). European populations of *C. melanoscela* introduced to the United States in the early part of the century (Burgess and Crossman 1929) have become naturalized and widely distributed throughout the expanding range of the gypsy moth in North America. Inundative releases of *C. melanoscela* have demonstrated the potential for an enhanced impact of this species in biological control programs (Weseloh and Anderson 1975). Release tactics investigated have included the use of hybridized strains (Hoy 1975) and sequential releases of parasitoids (Kolodny-Hirsch *et al.* 1988).

Naturalized populations of *C. melanoscela* in North America are subjected to high levels of cocoon- or hyperparasitism (Muesebeck and Dohanian 1927; Weseloh 1978). The annual mortality to *C. melanoscela* as a result of hyperparasitism may exceed 95% in southern Ontario (Bourchier and Nealis 1992). The high vulnerability to hyperparasitism of Ontario populations of *C. melanoscela* occurs because of the early induction of diapause in the local populations of the primary parasitoid (Nealis *et al.* 1995) combined with high rates of attack by the local hyperparasitoids (Bourchier and Nealis 1992). An inundative release tactic employing *C. melanoscela* in Ontario should consider these factors in order to maximize the impact of the released parasitoids.

Explorations in Asia for new biological control agents resulted in the collection, importation, and laboratory culture of an Asian population of *C. melanoscela* called the "halo" strain. The common name refers to the distinctive halo of silk which surrounds the cocoon (Weseloh 1982). Biological control workers have hoped that the silk halo could impede attack by hyperparasitoids and thus make this strain of *C. melanoscela* relatively less vulnerable to hyperparasitism. Weseloh (1982) found little evidence of differences in the vulnerability to hyperparasitism of the two strains of *C. melanoscela* in the laboratory or in field trials in Connecticut. His field trials, however, used parasitoid cocoons glued to a paper surface. Bourchier and Nealis (1992) have shown that hyperparasitism of *C. melanoscela* cocoons is highly dependent on microhabitat characteristics making it desirable to use a method of measuring hyperparasitism that closely mimics natural conditions when estimating rates of hyperparasitism. Weseloh (1982) also demonstrated that the two strains of *C. melanoscela* differed in their diapause characteristics. A Connecticut strain of the parasitoid entered diapause under photoperiods less than 16 h while the Asian strain was essentially diapause-free. Since his field exposures of both strains were for only 1 week, he did not address differences in vulnerability of the two strains arising from their different diapause characteristics. The short exposure time used by Weseloh also meant that the observed overall rate of hyperparasitism in his experiments was relatively low (less than 25%) compared to what would be expected under natural conditions (Bourchier and Nealis 1992).

In this paper, we extend Weseloh's (1982) results to compare the relative vulnerability to hyperparasitoids of a local Ontario strain of *C. melanoscela* with that of the Asian strain by exposing sentinel cocoons of both strains on a bark substrate to cocoon predators and hyperparasitoids under field conditions in Ontario. Based on these results, we make recommendations on a tactic for use of *C. melanoscela* in inundative releases against the gypsy moth in Ontario.

Materials and Methods

Insect colonies. Colonies of gypsy moth and the Ontario strain of *C. melanoscela* were initiated from natural populations near Sharbot Lake, Ontario, Canada. The Asian strain of *C. melanoscela* was obtained courtesy of Dr. M. Ticehurst of the National Gypsy Moth Management Group, Landisburg, Pennsylvania.

Both strains of *C. melanoscela* were maintained by exposing 2nd-instar gypsy moth to adult parasitoids and rearing the host and parasitoid on a standard artificial diet for gypsy moth (ODell *et al.* 1985). In general, all insects were reared at 22°C, 18L:6D. The need to synchronize the availability of large numbers of parasitoid cocoons for field exposures, however, required moving some cohorts of insects to 15°C or 28°C for short periods of time to either retard or hasten development. For Ontario *C. melanoscela*, an 18 h photoperiod was used to produce nondiapause cocoons and a 14 h photoperiod was used to produce diapause cocoons (Nealis *et al.* 1995). The Asian strain produced nondiapause cocoons at both 14 h and 18 h photoperiods (Weseloh 1982). Cocoons of the parasitoids were held at 10°C for up to one week before being taken to the field.

Field trials. Comparisons of hyperparasitism of Ontario and Asian cocoons were made in 1990 and 1991 at a field site in Olden Township, southeastern Ontario, Canada. A sentinel cocoon system was used in both years (Bourchier and Nealis 1992). This method consisted of a disk of red oak bark 8-cm in diameter to which approximately 10 cocoons of either the Ontario or Asian strain were attached. In 1990, most cocoons used were spun directly by the insects on to the bark disk. In 1991, most cocoons were glued to the bark disk. This enabled better use of reared

cocoons and provided a more standardized experimental unit. Care was taken to accept only those glued cocoons of the Asian strain for which the "halo" remained intact. Previous tests had shown that gluing had no effect on survival of the primary parasitoid or attack rates by hyperparasitoids (Bourchier and Nealis 1992).

One disk of each cocoon type was placed at breast-height on an oak tree for a pre-determined exposure period (Bourchier and Nealis 1992). Disks and cocoons were then retrieved and the cocoons placed individually in 7-dram shell vials and incubated in the laboratory for at least 30 days. As either the adult *C. melanoscela* or hyperparasitoids emerged, they were identified and recorded. When only a portion of a cocoon was recovered, the individual was scored as predated.

Following the 30-day incubation period, insects expected to be non-diapause (i.e. Asian strain or Ontario strain reared at L:D 18:6) were dissected to determine their fate. Insects expected to be in diapause were placed in cold-storage (2°C) for 4 months and then re-incubated (22°C). Emerging adult *C. melanoscela* or hyperparasitoids were identified and recorded. Cocoons from which no insects emerged after 30 days of post-diapause incubation were dissected to determine hyperparasitism.

For exposures longer than 1 week (1991 trials), some insect emergence occurred in the field. In most cases the emerged insect could be identified as either an adult *C. melanoscela* (i.e. no hyperparasitism) or a hyperparasitoid based on the shape of the emergence hole and the exuviae inside the cocoon. Because of the lack of specific identification for each hyperparasitoid, our analysis considered cocoons as simply hyperparasitized or not. The relative abundance of hyperparasitoid species in the area is given by Bourchier and Nealis (1992).

The 1990 trials tested the effect of cocoon morphology on natural mortality independent of diapause by comparing predation and hyperparasitism of nondiapause Ontario and Asian cocoons for relatively short exposure periods (3 to 5 days). Five trials were carried out between 28 June and 18 July. The 1991 trials compared hyperparasitism of diapause Ontario cocoons and nondiapause Asian cocoons for varying time periods between 3 and 25 July. The periods of exposure for these 1991 trials were: 5 days (3 to 8 July), 17 days (8 to 25 July), or 23 days (2 to 25 July). The 5-day trial in 1991 was a short exposure during which there was no natural emergence of adult parasitoids of either strain. This trial overlapped in time with the other 1991 trials. It thus provided a confirmation for the 1990 trials and a check for the other 1991 trials as diapause was not a factor in assessing vulnerability to hyperparasitism. The remaining 2 trials in 1991 were comparisons over longer time periods where the influence of diapause, and consequently a longer exposure period, could be examined.

Analysis. Data on cocoon vulnerability were organized in tables and analyzed by log-linear models using the log-likelihood ratio (G^2) as the test statistic. Inferences were based on the simplest, best-fit model for which the null hypothesis could not be rejected at a specified level. The analyses used the TABLES module of SYSTAT (Wilkinson 1990).

The relative frequency of predation of all cocoons for which at least some remnant of the cocoon was recovered was analyzed first. Predated cocoons were not included in the subsequent analyses of hyperparasitism. Cocoons from which neither an adult *C. melanoscela* nor a hyperparasitoid emerged, and dissection could not resolve the source of mortality with respect to hyperparasitism, were excluded from analyses of hyperparasitism.

Results

Field trials-predation. The short exposure periods used for cocoons in 1990 resulted in very little cocoon predation so the counts from all 5 trials were pooled for analysis. Only 12 of 656 (1.8%) cocoons of the Asian strain and 9 of 616 (1.5%) of the cocoons of the Ontario strain were removed by predators. There was no significant association between cocoon type and predation (G^2=0.26, df=1, p>0.10). The longer exposure periods of 1991 resulted in higher overall levels of predation; 46 of 537 (8.6%) of cocoons of the Asian strain and 54 of 511 (10.6%) of cocoons of the Ontario strain but as in 1990, there was no significant association between cocoon type and predation (G^2=1.22, df=1, p>0.10). Thus predation rates were comparable on both cocoon types.

Field trials-hyperparasitism. The 1990 data were analyzed by a three-way table [exposure period (5 trials) by cocoon type or strain (Asian *vs* Ontario) by hyperparasitism (yes or no)]. There was no evidence of a three-way interaction (G^2=6.50, df=4, p>0.10). The simplest, best-fit model involved only the association between trial and hyperparasitism (G^2=72.1, df=8, p<0.01); the overall frequency of hyperparasitism was greater later in the season (Fig. 1). For the short exposure periods, the frequency of hyperparasitism was independent of the strain (Ontario or Asian) of nondiapause cocoons.

There was a marginal association between cocoon type and hyperparasitism in the short exposure trial (5 days) in 1991 (G^2=4.26, df=1, p=0.04) but the difference between rates of hyperparasitism on different cocoon types was not large (Fig. 2). The association was definitely significant in the 17-day exposure (trial 2: G^2=14.88, df=1, p<0.01) and even more so in the 23-day exposure (trial 3: G^2=35.34, df=1, p<0.01). The observed differences in hyperparasitism between strains in the longer exposures are conservative because diapause Ontario cocoons were removed before all hyperparasitism was completed (28 July). Under natural conditions, hyperparasitism rates on these diapause cocoons would be even higher because the cocoons would have remained vulnerable to hyperparasitism throughout the season (Bourchier and Nealis 1992). In contrast, when nondiapause Asian cocoons were collected from the field, they had either been hyperparasitized or the primary parasitoid had successfully emerged. No further increases in hyperparasitism would have been possible even if the exposure time had been increased.

Discussion

The effectiveness of inundative releases of parasitoids in biological control can be greatly enhanced by utilizing biological and ecological knowledge to improve the tactical aspects of the release. In this study, we show that the distinctive cocoon characteristic of the Asian or "halo" strain of *C. melanoscela* does not, in itself, render the Asian strain less vulnerable to either predation or hyperparasitism in Ontario. These results provide critical field confirmation of the results of Weseloh (1982), tested against the hyperparasitoid fauna of southern Ontario. This study does show, however, that another intrinsic characteristic of the Asian strain of *C. melanoscela*, namely its lack of diapause, reduces the vulnerability of this strain to hyperparasitism by reducing the period of exposure of the cocoon to hyperparasitoids. Bourchier and Nealis (1992) showed that the early onset of diapause in Ontario populations of *C. melanoscela* extends exposure of the vulnerable cocoon stage to hyperparasitism. The cumulative effect of the high attack rates by hyperparasitoids throughout the summer results in losses of over 95% of the beneficial, primary parasitoid. Inundative releases of strains which do not diapause would reduce these losses to hyper-

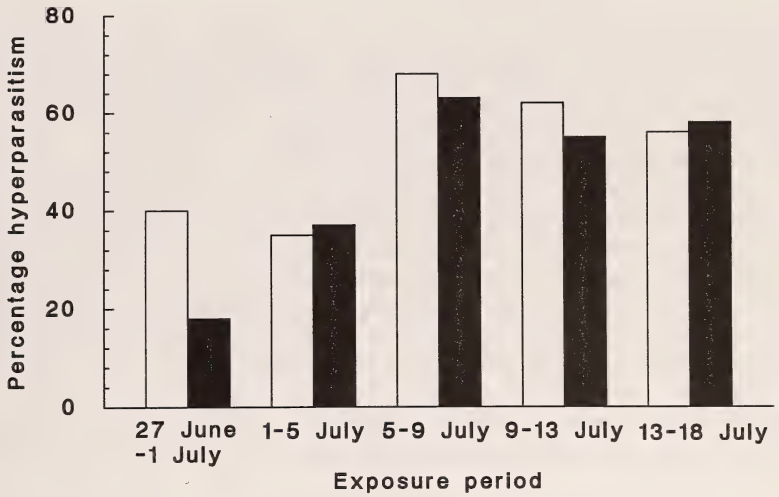

FIGURE 1. Percentage hyperparasitism of sentinel cocoons of Asian (open bars) and Ontario (solid bars) strains of *Cotesia melanoscela* exposed for less than 1 week on oak trees in Olden Township, Ontario, 1990. Percentages are based on sample sizes ranging from a minimum of 40 cocoons of the Ontario strain in the earliest trial to a maximum of 241 cocoons of the Asian strain in the latest trial. In all trials, the rate of hyperparasitism was independent of the type of cocoon ($p>0.10$).

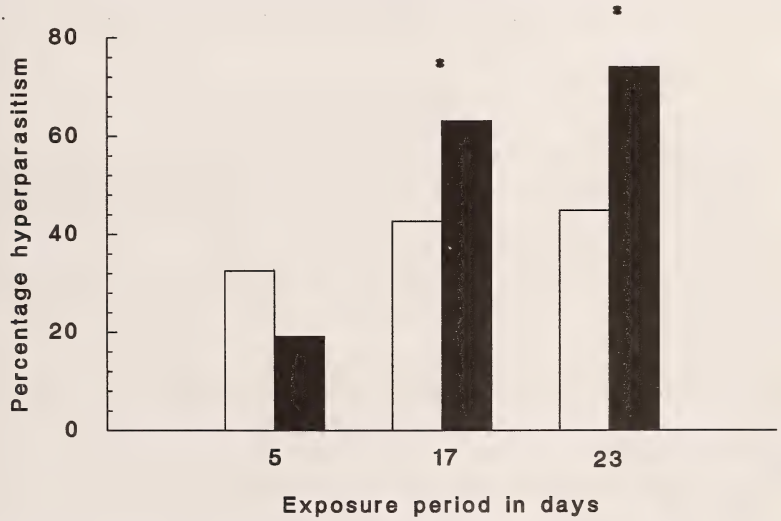

FIGURE 2. Percentage hyperparasitism of sentinel cocoons of Asian (open bars) and Ontario (solid bars) strains of *Cotesia melanoscela* exposed for varying periods of time on oak trees in Olden Township, Ontario, 1991. See methods section for details on exposure periods. Percentages are based on sample sizes ranging from a minimum of 89 cocoons of each strain in the 5-day trial to a maximum of 205 cocoons of the Asian strain in the 23-day trial. Asterisks over bars indicate trials for which there was a significant association between hyperparasitism and type of cocoon at $p<0.01$.

parasitism particularly in areas such as Ontario where *C. melanoscela* is largely univoltine (Nealis *et al.* 1995). It would not be necessary to use exotic strains of *C. melanoscela* since the diapause response in local strains can be readily manipulated by varying the photoperiod during development of the parasitoid larvae (Weseloh 1973; Nealis *et al.* 1995).

A second recommendation for inundative releases arising from these studies is the timing of release. Bourchier and Nealis (1992) show that, in Ontario, hyperparasitoid activity does not commence until mid-June and is greatest in July and early August. This was confirmed in this study. Inundative releases of parasitoid adults as early as vulnerable gypsy moth larvae become available in the spring could also minimize losses of cocoons to hyperparasitism by ensuring that cocoon phenology does not overlap with the period of maximum hyperparasitoid activity. Use of nondiapause strains in these early inundative releases would have the added benefit of providing the possibility of a second, natural generation of primary parasitoids in time to make additional attacks on the gypsy moth population. Studies of bivoltine populations of *C. melanoscela* indicate that additional attacks by a second generation of parasitoids can occur although the rate of attack is reduced because of reduced susceptibility to parasitoid attacks by late-instar gypsy moth larvae (Weseloh 1976).

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FORAGING BEHAVIOUR OF HONEY BEES (*APIS MELLIFERA*) ON ASPARAGUS (*ASPARAGUS OFFICINALIS*)

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Abstract *Proc. ent. Soc. Ont.* 126: 37-43

We investigated the foraging behaviour of honey bees on a dioecious crop plant, *Asparagus officinalis* L., in reference to seed production. Mostly, the honey bees foraged along only one row and only later in the day was there even a slight tendency for the bees to switch between rows. In the morning, the bees, on average, visited the flowers of only three plants but by late afternoon visited, on average, the flowers of six plants. The number of flowers visited per plant decreased from an average of 13.6 to 2.3 with sequentially visited plants (1st to 6th). The bees did not appear to behave differently on male and female plants. Because honey bees are likely to be the most important pollinator for seed production in asparagus, it is recommended that male and female plants be grown in the same rows, with every tenth plant being male.

Introduction

Asparagus (*Asparagus officinalis* L. Asparagaceae) is a minor crop in Ontario. In 1994, 1.5 million kg of asparagus worth 4 million dollars were harvested from 845 hectares. For several years, research has been funded at the University of Guelph to increase asparagus production by improving agronomic practices and by developing hybrids.

Although hermaphrodite flowers sometimes occur, *A. officinalis* is functionally a dioecious species with staminate and pistillate flowers on different plants. Flowers are small (the staminate ones are slightly larger than the pistillate ones) and with a greenish-white perianth. The staminate flower has six stamens which are rudimentary in the pistillate flower. The pollen is typically orange. Pistillate flowers have a style with three stigmas, and in both sexes the nectaries are at the base of the perianth segments (Free 1970).

In this species, cross-pollination is essential for fruit set. Jones and Rosa (1928) thought that honey bees were the main insect pollinators and that wind was a negligible factor in pollination. This was confirmed by Eckert (1956) who made exclusion experiments and obtained much less seed on caged plants than on plants outside the cages. Kraai (1962) was able to cross-pollinate asparagus with small queenless colonies of honey bees that had two or three combs with plenty of brood.

For asparagus production, pollination is not an issue and male plants are preferred because they produce more, even though female ones have larger spears (Ellison 1986). However, one of the challenges in producing asparagus seed is the arrangement of male and female plants in the

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field. Even though male and female plants are equally abundant in natural populations, seed crops can be produced with only one male for every five or six females (Hawthorn and Pollard 1954). Huyskes (1959) found that a male plant pollinates those females within a 5 meter radius. However, the distribution of the sexes in the field is as important as the sex ratio. Two general patterns may be considered: a) one row of male plants for every *x* rows of female plants, or b) male and female plants in the same row.

It is well known that bees do not forage randomly, but move in an energetically optimal pattern (Pyke 1978, 1979; Waddington and Heinrich 1981). Understanding the foraging behaviour of honey bees can help to decide which of the planting schemes mentioned above would produce more seeds. Thus, the aim of our paper is to study the foraging pattern of this pollinator on asparagus, in order to determine how best to arrange female and male plants in the field for seed production.

Materials and Methods

The observations were made on asparagus plants planted in blocks in experimental plots located at Agricultural Research Stations at Arkell and Cambridge in Southern Ontario, Canada during June and July, 1994. Most of the observations on male plants were made in Cambridge because this sex was relatively scarce at Arkell. However, most of our observations were made on female plants, and these were sampled equally at both research stations.

Two different kinds of observations were made:

a) The observer stood at the end of the central row of three randomly chosen rows in a block. Honey bees foraging any of the rows were followed until they left the block.

b) The observer stood between two rows. Honey bees entering either of the two rows were followed either from the left or the right side and were followed until they left an area delimited by four rows (Fig. 1).

The following information was recorded: Number of rows visited by the honey bee; number of plants visited per row and the number of flowers visited per plant. In addition, some flowers were bagged one night to collect nectar samples the following day. The observations were made from 9 am to 5 pm. The nectar samples were collected twice a day, in the morning at 10 am and again in the afternoon at 4 pm.

Statistical analyses were carried out using χ^2 approximation of the Kruskall-Wallis test ($\chi^2_{(kw)}$), χ^2 test of independence and χ^2 goodness of fit to compare frequency distributions. Null hypotheses with a probability of acceptance of less than 5% were rejected.

Results

During the observations, honey bees were almost the only insects noted on the flowers. Although other Hymenoptera were seen hovering over the plants, none was observed on the blossoms.

In our study, no significant difference was found in nectar secretion either between males and females or morning and afternoon (χ^2=1.93, p=0.0953) (Table I).

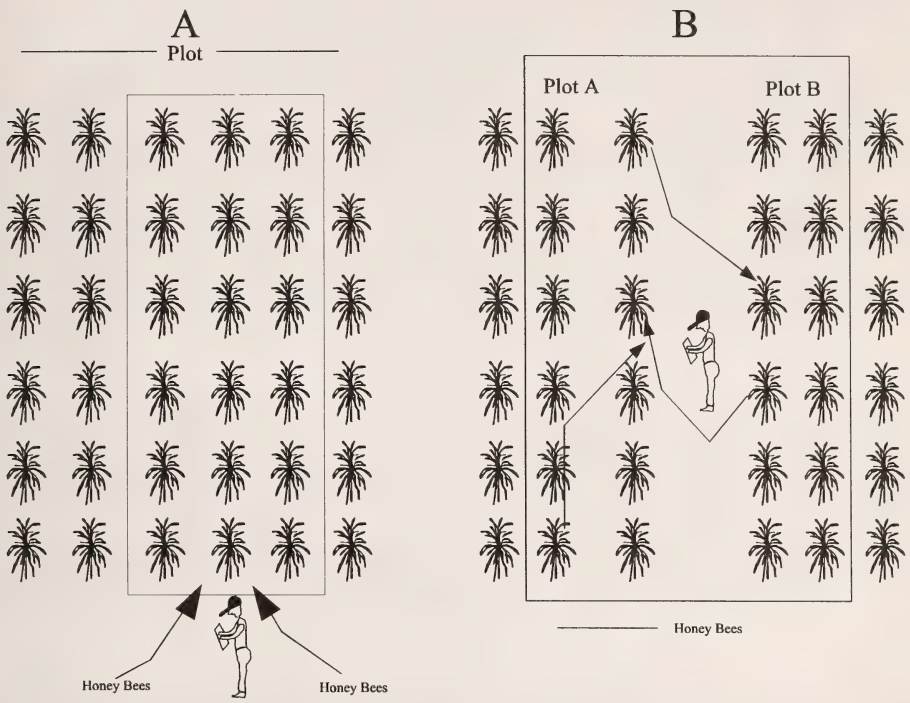

FIGURE 1. Schemes showing how the observations were made. (A) Observations made starting standing at one end of the row; (B) observations made starting in the middle of two rows. The rectangles indicate the area sampled and in which the observations were made.

Nothing suggested that the foraging pattern of honey bees depended on the sex of the plant. Few males were sampled and consequently, in the preliminary analyses of the data, observations on male and female plants were pooled. The calculated variances were low (coefficients of variation in the range of 13 to 20%).

During a single foraging bout, a significantly higher number of honey bees was observed foraging on only one row than was observed on two, three or more rows ($\chi^2_{(kw)}$=2.17, $p<0.0001$, n=168) (Fig. 2). Figure 3 shows the number of plants visited/row when one, two or three rows were visited (n=168). When more than one row was worked by the bee, fewer plants (Fig. 3) and fewer flowers/plant (Fig. 4) were visited per each extra row. When only one row was visited, the average number of flowers foraged/plant decreased with an increase in the number of plants visited (Table II). The variation in the number of flowers worked/plant also decreased (Fig. 5).

The number of plants visited per row depended upon where the bees had begun foraging (χ^2=27.13, $p<0.001$, n=168) (Fig. 6). The highest proportion of bees that had begun foraging from the end of the row visited three plants per row, whereas the highest proportion of bees that had begun foraging in the middle of the row visited only one plant per row.

TABLE I. Volume of nectar in bagged male and female flowers of *Asparagus officinalis* in the morning and in the afternoon.

	Morning	Afternoon
Male	0.83±0.16 μl (*n*=63)	1.03±0.8 μl (*n*=61)
Female	0.76±0.17 μl (*n*=63)	1.12±0.2 μl (*n*=61)

The number of rows visited in a foraging bout depended on the time of day and fewer bees were observed foraging one row in the morning compared to the afternoon.

Discussion

In our study, honey bees presented the following foraging pattern on asparagus: in almost all (approximately 95%) foraging bouts, the honey bee entered from the end of the row and foraged usually along only one row visiting on average three plants per row. However, this pattern varied according to the availability of resource (time of day).

Any difference between the volume of nectar secreted by male or female plants during the day may determine to a great extent the foraging pattern of the honey bees (Greco *et al.* in press) but no difference was found in the secretion of nectar between either sexes or time of day.

TABLE II. Mean number of flowers worked per plant for different numbers of plants visited when only one row is foraged (figures in parentheses represent coefficients of variation)

	1 plant	2 plants	3 plants	4 plants	5 plants	6 plants
1st plant	13.6±4.47 (40%)	15.6±9.7 (62%)	6.5±3.53 (54%)	3.5±0.70 (20%)	6±1.41 (23%)	3.2±0.6 (18%)
2nd plant		1.3±0.6 (43%)	3±1.41 (47%)	1.5±0.60 (40%)	3.5±1.12 (32%)	2.1±0.5 (24%)
3rd plant			1.5±0.7 (47%)	2.5±0.82 (33%)	1.3±0.67 (51%)	1.1±0.3 (28%)
4th plant				2.7±0.8 (29%)	1.6±0.7 (43%)	2.3±0.7 (31%)
5th plant					1.2±0.4 (35%)	2.5±0.8 (32%)
6th plant						2.7±1.2 (44%)
Average	13.6±4.47 (40%)	8.5±9.97 (117%)	3.6±2.6 (73%)	2.5±1.0 (39%)	2.7±0.76 (28%)	2.3±1.2 (33%)

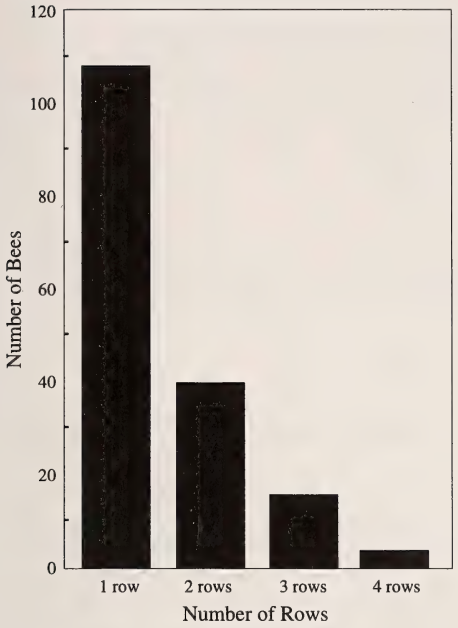

FIGURE 2. Number of honey bees observed foraging only one, two, three or four rows of *Asparragus officinalis* (n=168).

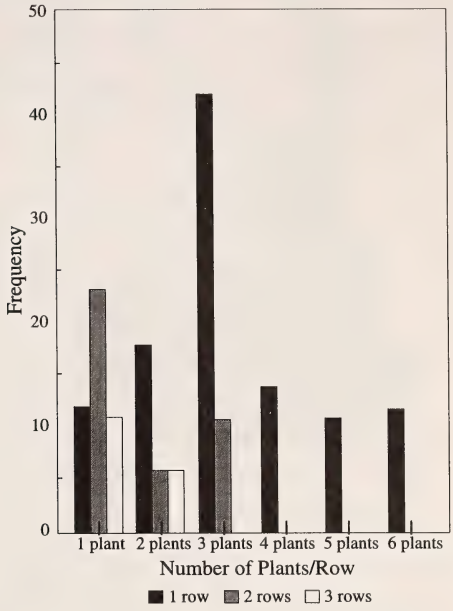

FIGURE 3. Number of plants per row visited in a foraging bout of a honey bee foraging on one, two or three rows (n=168).

Honey bees visited four to six plants/row in the late afternoon when a high percentage of the flowers were probably already depleted of nectar. Nectar availability would seem higher in the morning (Table I). When the amount of nectar is high in a given area, honey bees tend to hover in that small area and perform short, jagged flights, visiting more flowers per plant and reducing the number of plants visited. Instead, when the resources are scarce, they fly longer distances (Butler *et al.* 1943; Ribbands 1949; Schmidt-Hempel 1984). This might explain the reduction in the average and variance in the number of flowers visited per plant when the number of plants foraged increases. This also might explain the relationship between the number of rows visited and the time of day when the observation was made. This is likely an indirect relationship mediated by the amount of nectar available.

As the number of plants visited per row is smaller for a second or third row visited, the difference found in frequency distribution in plants/row between honey bees sampled in one end of the row and those sampled in the middle may indicate that honey bees initiate their foraging bouts more often at either end of the row instead of at any place in the middle.

Because honey bees forage mostly along rows and because of the shape of the frequency distribution of the number of plants visited/row, alternating male plants between several female ones seems to be the best planting arrangement to secure high seed sets. Further, bees were sel-

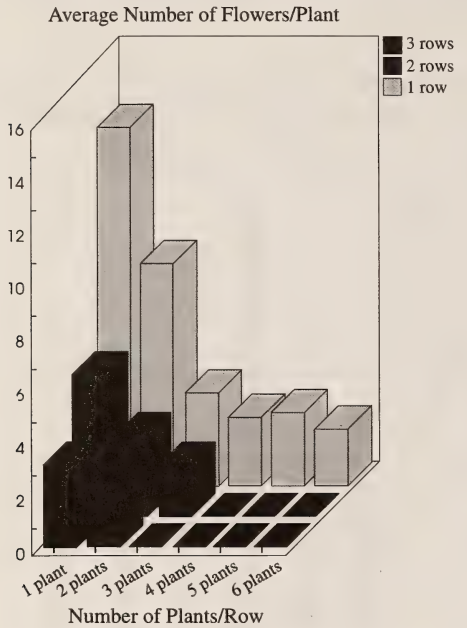

FIGURE 4. Average number of flowers per plant visited by a honey bee when one to three rows and one to six plants per row are foraged.

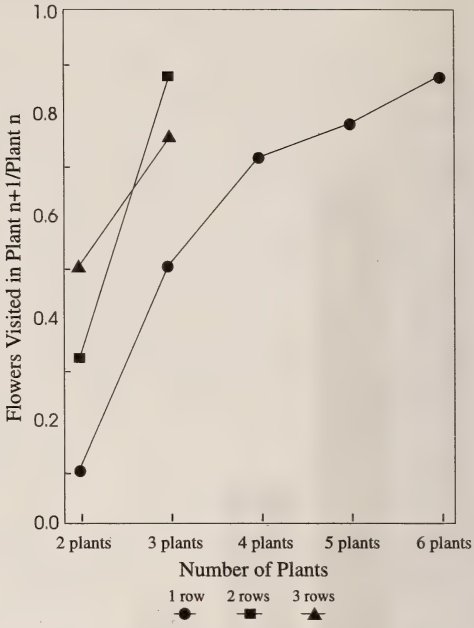

FIGURE 5. Variation of the ratio "flowers visited in plant n/plant n+1" as a function of the number of plants foraged for honey bees visiting either one, two or three rows in a foraging bout.

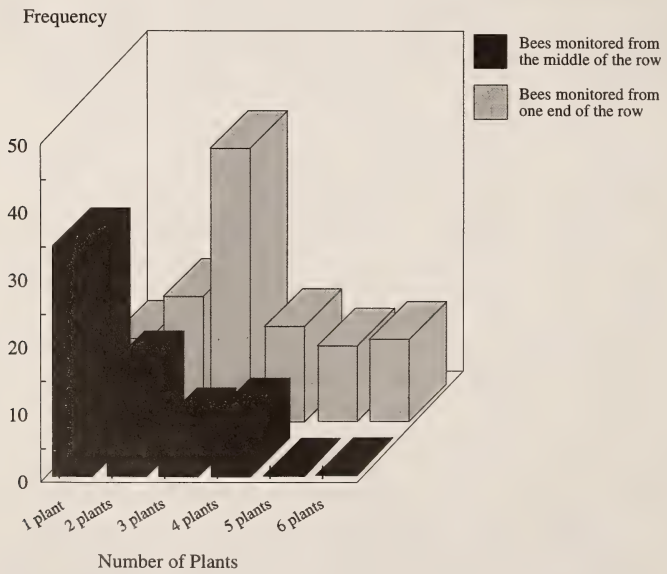

FIGURE 6. Difference in the frequency distribution of the number of plants visited per row for bees monitored in one extreme of the row and in the middle of the row.

dom observed to skip plants in the row (this was more frequently observed towards the end of the day); therefore, to put male plants as every tenth one and at the ends of each row can be an efficient way to distribute the sexes in the field. This may also help to increase the probability of a bee loaded with pollen, coming from a nearby row, to forage on a female plant. This foraging model, however, needs to be substantiated experimentally in fields with asparagus planted with the suggested distribution.

Acknowledgements

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CHECKLIST OF COLLEMBOLA (INSECTA: APTERYGOTA) OF CANADA AND ALASKA

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Abstract *Proc. ent. Soc. Ont.* 126: 45-76

Four hundred and twelve species of Canadian and Alaskan Collembola arranged in 16 families and 83 genera are listed with all known provincial and state records. The estimate of 412 species should be considered conservative. Species of questionable status or those identified only to genus were omitted. The lack of Collembola species records for Prince Edward Island and the few records for Yukon, Saskatchewan, New Brunswick, and Newfoundland reflects a collecting deficiency rather than an absence of Collembola.

Introduction

The Collembola (springtails) are small, wingless arthropods that occur in almost all terrestrial habitats and the littoral. They are a major factor in soil formation and may also be found in decaying vegetable matter, among herbage, under tree bark and similar environments. They are often abundant, and occasionally injurious to plants. The snow-flea, *Hypogastrura nivicola* (Fitch), is sometimes extremely abundant on the surface of the snow, especially in early spring. *Podura aquatica* Linnaeus is often seen in great numbers along the margins of ponds and streams, and *Anurida maritima* (Guerin-Meneville) is found in abundance along the seashore and is daily submerged by each tide. The major condition which is essential for their welfare is an ample amount of moisture, for Collembola are rare in dry situations.

Over 2000 species have been described throughout the world. The collembolan fauna of Canada and Alaska has never been systematically treated or catalogued. The scattered distributional records and the few taxonomic treatments have been summarized by Christiansen and Bellinger (1980-1981). The entries in this checklist were obtained by extracting appropriate geographical records from Christiansen and Bellinger (1980-1981) and reviewing available literature to December 31, 1994. Additional data were obtained by examining identified specimens in the Canadian National Collection of Insects at Ottawa.

I intend to update this checklist periodically and I would appreciate receiving reprints or other data relevant to the Canadian and Alaskan collembolan fauna, and having any errors or omissions in this checklist brought to my attention. I hope this checklist will encourage research on the taxonomy and geographical distribution of this important group of insects.

The classification adopted here closely follows that in Christiansen and Bellinger (1980-1981) with subsequent improvements principally from Mari Mutt and Bellinger (1990). Currently 412 species of Collembola, distributed in 16 families and 83 genera, are known from Canada and Alaska. Species are listed in alphabetical order. Synonyms are not included. Records are shown as follows: ALASKA (193); YUKON TERRITORIES (11); NORTHWEST TERRITORIES (107);

BRITISH COLUMBIA (148); ALBERTA (55); SASKATCHEWAN (3); MANITOBA (71); ONTARIO (129); QUEBEC (68); NEW BRUNSWICK (6); NOVA SCOTIA (32); PRINCE EDWARD ISLAND (0); NEWFOUNDLAND (14).

Acknowledgements

I am very grateful to D.E. Bright for allowing me time to pursue this project and for invaluable advice and assistance during the preparation of this checklist. Anthony Davies and Larry Speers provided valuable support with the computer program. Susan Sherman and Steve Gammon assisted with the literature search and innumerable literature requests. Dr. Kenneth Christiansen was of great help in supplying me with many new distribution records. Dr. Valin G. Marshall reviewed the manuscript and made many useful suggestions.

ORDER COLLEMBOLA

SUBORDER ARTHROPLEONA

FAMILY PODURIDAE

Genus *PODURA* Linné 1758: 608

P. aquatica Linné 1758: 609	AK	-	NT	BC	-	-	-	ON	-	-	-	-	-

FAMILY HYPOGASTRURIDAE
Subfamily Hypogastrurinae

Genus *HYPOGASTRURA* Bourlet 1839: 404
Subgenus *Cyclograna* Yosii 1961a: 250

H. horrida Yosii 1960: 266	AK	-	-	BC	-	-	-	-	-	-	-	-	-
H. krafti (Scott) 1962: 238	AK	-	-	BC	-	-	-	-	-	-	-	-	-
H. loricata Yosii 1960: 264	AK	-	-	-	-	-	-	-	-	-	-	-	-
H. virga Christiansen & Bellinger 1980-1981: 183	AK	-	-	-	-	-	-	-	-	-	-	-	-
H. vulgaris Yosii 1960: 263	AK	-	-	BC	-	-	-	-	-	-	-	-	-
H. wallmoi Fjellberg 1985a: 50	AK	-	-	BC	-	-	-	-	-	-	-	-	-
Subgenus *Hypogastrura* (s. str.)													
H. christianseni Yosii 1960: 269	-	-	-	-	AB	-	-	-	-	-	-	-	-
H. concolor (Carpenter) 1900: 272	AK	-	-	-	-	-	-	-	-	-	-	-	-
H. copiosa (Folsom) 1916: 480	-	-	-	-	-	-	-	ON	-	-	-	-	-
H. devia Christiansen & Bellinger 1980-1981: 66	AK	-	-	-	-	-	-	-	-	-	-	-	-
H. distincta (Axelson) 1902: 104	AK	-	-	-	-	-	-	-	-	-	-	-	-

H. essa Christiansen & Bellinger 1980-1981: 68	AK	-	-	-	-	-	-	-	-	-	-	-	-	-
H. harveyi (Folsom) 1902d: 320	-	-	-	-	-	-	-	ON	-	-	-	-	-	-
H. helena Christiansen & Bellinger 1980-1981: 118	AK	-	-	-	-	-	-	-	-	-	-	-	-	-
H. humi (Folsom) 1916: 489	AK	-	NT	-	-	-	-	ON	-	-	-	-	-	-
H. ireneae (Wray) 1953a: 2	AK	-	-	-	-	-	-	-	-	-	-	-	-	-
H. litoralis (Linnaniemi) 1909: 16	AK	-	-	-	-	-	-	-	-	-	-	NS	-	-
H. macrotuberculata (Hammer) 1953b: 13	AK	-	NT	-	-	-	MB	ON	QC	-	-	-	-	-
H. manubrialis (Tullberg) 1869: 9	AK	-	NT	-	-	-	MB	ON	-	-	-	-	-	-
H. manubrialis assimilis (Krausbauer) 1898: 503	-	-	NT	-	-	-	MB	-	-	-	-	-	-	-
H. matura (Folsom) 1916: 481	-	-	-	BC	-	-	-	-	-	-	-	-	-	-
H. nivicola (Fitch) 1846: 283	AK	-	-	BC	AB	-	-	ON	QC	-	-	-	-	-
H. notha (Macnamara) 1922: 152	-	-	-	-	-	-	-	ON	QC	-	-	-	-	-
H. oregonensis Yosii 1960: 276	AK	-	-	-	-	-	-	-	-	-	-	-	-	-
H. packardi (Folsom) 1902d: 319	-	-	-	-	-	-	-	ON	-	-	-	-	-	-
H. pannosa (MacNamara) 1922: 153	AK	-	NT	BC	-	-	-	ON	-	-	-	-	-	-
H. perplexa Christiansen & Bellinger 1980-1981: 124	AK	-	-	-	-	-	-	ON	-	-	-	-	-	-
H. purpurescens (Lubbock) 1868: 302	-	-	-	BC	-	-	-	ON	-	-	-	-	-	-
H. ripperi Gisin 1952: 1	AK	-	-	-	-	-	-	-	-	-	-	-	-	-
H. sensilis (Folsom) 1919: 5a	AK	-	NT	-	-	-	-	-	-	-	-	-	-	-
H. spitsbergensis (Stach) 1962: 5	AK	-	-	-	-	-	-	-	-	-	-	-	-	-
H. tooliki Fjellberg 1985a: 30	AK	-	-	-	-	-	-	-	-	-	-	-	-	-
H. trybomi (Schött) 1893: 82	AK	-	NT	BC	-	-	-	-	-	-	-	-	-	-
H. tullbergi (Schäffer) 1900: 244	AK	-	NT	BC	-	-	MB	ON	-	-	-	-	-	-
H. utahensis (Wray) 1953a: 4	-	-	-	BC	-	-	-	-	-	-	-	-	-	-
H. viatica (Tullberg) 1872: 50	-	-	NT	-	-	-	MB	-	QC	-	-	-	-	-
Subgenus *Mitchellania* Wray 1953: 1														
H. gibbomucronata (Hammer) 1953b: 17	-	-	NT	-	-	-	-	-	-	-	-	-	-	-
H. virga Christiansen & Bellinger 1980-1981: 183	-	-	-	BC	-	-	-	-	-	-	-	-	-	-
H. vulgaris Yosii 1960: 263	-	-	-	BC	-	-	-	-	-	-	-	-	-	-
Subgenus *Mucrella* Fjellberg 1985a: 12														
H. arborea Fjellberg 1992: 405	-	-	-	BC	-	-	-	-	-	-	-	-	-	-
H. denali Fjellberg 1985a: 13	AK	-	-	-	-	-	-	-	-	-	-	-	-	-
Genus *CERATOPHYSELLLA* Börner 1932: 140														
C. armata (Nicolet) 1842: 57	AK	-	NT	BC	-	-	MB	ON	-	-	-	-	-	-
C. boletivora (Packard) 1873: 30	-	-	-	-	AB	-	-	-	-	-	-	-	-	-

C. brevis (Christiansen & Bellinger) 1980-1981: 155	AK	-	-	-	-	-	-	ON	-	-	-	-	-
C. brevisensillata Yosii 1961a: 251	AK	-	-	-	-	-	-	-	-	-	-	-	-
C. czukczorum (Martynova & Bondarenko) 1978: 48	AK	-	NT	-	-	-	-	-	-	-	-	-	-
C. denticulata (Bagnall) 1941: 218	AK	-	NT	BC	AB	-	MB	ON	QC	-	-	-	-
C. glancei Hammer 1953b: 18	AK	-	NT	-	-	-	-	-	-	-	-	-	-
C. guthriei (Folsom) 1916: 489	-	-	-	-	-	-	-	ON	-	-	-	-	-
C. isabellae Fjellberg 1985a: 43	AK	-	-	-	-	-	-	-	-	-	-	-	-
C. longispina (Tullberg) 1876: 37	AK	-	-	-	-	-	-	-	-	-	-	-	-
C. maheuxi (Butler) 1966: 683	-	-	-	-	-	-	-	-	QC	-	-	-	-
C. palustris (Martynova) 1978: 27	AK	-	-	-	-	-	-	-	-	-	-	-	-
C. pecki (Christiansen & Bellinger) 1980-1981: 163	AK	-	-	-	AB	-	-	-	-	-	-	-	-
C. pseudarmata (Folsom) 1916: 490	-	-	-	BC	AB	-	MB?	-	-	-	-	-	-
C. revispina (Harvey) 1893a: 182	-	-	-	-	-	-	-	-	-	NB	-	-	-
C. scotti (Yosii) 1962: 14	AK	-	-	-	-	-	-	-	-	-	-	-	-
C. succinea (Gisin) 1949: 393	AK	-	NT	-	AB	-	-	-	-	-	-	-	-
Genus *SCHOETELLA* Schäffer 1896: 175															
S. glasgowi (Folsom) 1916: 494	-	-	-	-	-	-	-	ON	-	-	-	-	-
S. ununguiculata (Tullberg) 1869: 11	-	-	-	-	-	-	-	-	QC	-	-	-	-
Genus *BONETOGASTRURA* Thibaud 1975: 345															
B. variabilis (Christiansen) 1952: 125	AK	-	-	-	-	-	-	-	-	-	-	-	-
Genus *KNOWLTONELLA* Wray 1958: 1															
K. idahoensis Wray 1958: 1	-	-	-	-	AB	-	-	-	-	-	-	-	-
Genus *MICROGASTRURA* Stach 1922b: 113															
M. minutissima (Mills) 1934: 14	AK	-	-	-	-	-	-	-	-	-	-	-	-
Genus *SCHAEFFERIA* Absolon 1900: 265															
Subgenus *Schaefferia* (s. str.)															
S. cheoha Wray 1963:103	-	-	-	BC	-	-	-	-	-	-	-	-	-
S. duodecimocellata Bonet 1945: 19	AK	-	-	-	-	-	-	-	-	-	-	-	-
Genus *TYPHLOGASTRURA* Bonet 1930: 126															
T. variabilis Christiansen 1952: 125	AK	-	-	-	-	-	-	-	-	-	-	-	-
Genus *STENOGASTRURA* Christiansen & Bellinger 1980-1981: 207															
S. hiemalis Christiansen & Bellinger 1980-1981: 208	-	-	-	-	-	-	-	-	-	-	NS	-	-
Genus *TRIACANTHELLA* Schäffer 1897: 14															
T. copelandi (Wray) 1963: 101	-	-	-	-	-	-	-	ON	-	-	-	-	-

Genus *WILLEMIA* Börner 1901b: 428													
W. arida Fjellberg 1991c: 205	AK	-	-	BC	AB	-	-	-	-	-	-	-	-
W. anophthalma Börner 1901b: 428	AK	-	NT	-	-	-	-	ON	QC	-	-	-	-
W. biseta Christiansen & Bellinger 1980-1981: 237	-	-	-	BC	-	-	-	-	-	-	-	-	-
W. denisi Mills 1932: 263	AK	-	NT	BC	AB	-	-	-	-	-	-	-	-
W. granulata Fjellberg 1985a: 64	AK	-	-	-	-	-	-	-	-	-	-	-	-
W. intermedia Mills 1934: 17	-	-	-	BC	-	-	-	-	QC	-	-	-	-
W. scandinavica Stach 1949: 244	AK	-	-	-	-	-	-	-	-	-	-	-	-
W. similis Mills 1934: 19	AK	-	NT	-	-	-	-	-	-	-	-	-	-
Genus *XENYLLA* Tullberg 1869: 11													
X. affiniformis Stach 1929: 280	-	-	-	BC	-	-	-	-	-	-	-	-	-
X. betulae Fjellberg 1985a: 58	AK	-	-	-	-	-	-	-	-	-	-	-	-
X. canadensis Hammer 1953b: 20	AK	-	NT	-	-	-	MB	-	-	-	-	-	-
X. humicola (O. Fabricius) 1780: 213	AK	-	-	BC	AB	-	MB	ON	QC	-	-	-	-
X. pseudomaritima James 1933: 87	-	-	-	-	-	-	-	ON	-	-	-	-	-
FAMILY ODONTELLIDAE													
Genus *ODONTELLA* Schäffer 1897: 9 Subgenus *Odontella* (s. str.)													
O. biloba Christiansen & Bellinger 1980-1981: 254	-	-	-	BC	-	-	-	-	-	-	-	-	-
O. cornifer Mills 1934: 25	AK	-	-	BC	-	-	-	-	-	-	-	-	-
O. rossi Christiansen & Bellinger 1980-1981: 261	-	-	-	BC	-	-	-	-	-	-	-	-	-
O. shasta Christiansen & Bellinger 1980-1981: 263	-	-	-	BC	-	-	-	-	-	-	-	-	-
O. substriata Wray 1952: 104	-	-	-	BC	-	-	-	-	-	-	-	-	-
Genus *XENYLLODES* Axelson 1903: 3													
X. armata Axelson 1903: 4	AK	-	NT	BC	-	-	MB	-	-	-	-	-	NF
X. wapiti Fjellberg 1985b: 131	AK	-	-	-	-	SK	-	-	-	-	-	-	-
FAMILY NEANURIDAE Subfamily Brachystomellinae													
Genus *BRACHYSTOMELLA* Ågren 1903: 127													
B. parvula (Schäffer) 1896: 176	AK	-	-	BC	-	-	-	-	-	-	-	-	-
B. stachi Mills 1934: 19	-	-	-	BC	-	-	-	-	-	-	-	-	-

Subfamily Frieseinae

Genus *FRIESEA* Dalla Torre 1895: 14														
F. alaskella Fjellberg 1985a: 71	AK	-	-	-	-	-	-	-	-	-	-	-	-	
F. claviseta Axelson 1900: 112	AK	-	-	-	-	-	-	ON	-	-	-	-	-	
F. millsi Christiansen & Bellinger 1974: 389	AK	-	-	BC	AB	-	-	-	-	-	-	-	-	
F. mirabilis (Tullberg) 1871: 155	AK	-	-	-	-	-	-	ON	QC	-	-	-	-	
F. quinta Christiansen & Bellinger 1974: 392	-	-	-	BC	-	-	-	-	-	-	-	-	-	
F. quinquespinosa Wahlgren 1900: 368	AK	-	-	-	-	-	-	-	-	-	-	-	-	
F. sublimis MacNamara 1921: 128	-	-	NT	-	-	-	MB	ON	QC	-	-	-	-	
F. wilkeyi Christiansen & Bellinger 1974: 393	-	-	-	BC	-	-	-	-	-	-	-	-	-	

Subfamily Pseudachorutinae

Genus *PSEUDACHORUTES* Tullberg 1871: 155														
Subgenus *Pseudachorutes* (s. str.)														
P. aureofasciatus (Harvey) 1898: 216	-	-	-	BC	AB	-	-	ON	QC	-	-	-	-	
P. columbicus Rusek 1991: 120	-	-	-	BC	-	-	-	-	-	-	-	-	-	
P. corticicolus (Schäffer) 1897: 176	-	-	-	BC	-	-	-	-	-	-	-	-	-	
P. curtus Christiansen & Bellinger 1980-1981: 232	-	-	-	BC	-	-	-	-	-	-	-	-	-	
P. dilatatus (MacGillivray) 1893b: 317	-	-	-	-	-	-	-	-	QC	-	-	-	-	
P. indiana Christiansen & Bellinger 1980-1981: 312	AK	-	-	-	-	-	-	-	-	-	-	-	-	
P. lunatus Folsom 1916: 501	-	-	-	BC	-	-	-	ON	-	-	-	-	-	
P. saxatilis MacNamara 1920: 174	-	-	-	BC	-	-	-	ON	-	-	-	-	-	
P. simplex Maynard 1951: 59	-	-	-	-	-	-	-	-	QC	-	-	-	-	
P. subcrassoides Mills 1934: 24	AK	-	-	BC	AB	-	MB	ON	-	-	-	-	-	
Genus *ANURIDA* Laboulbène 1865: 199														
Subgenus *Anurida* (s. str.)														
A. amorita Folsom 1902a: 90	AK	-	-	-	-	-	-	-	-	-	-	-	-	
A. beringi Fjellberg 1985a: 101	AK	-	-	-	-	-	-	-	-	-	-	-	-	
A. decemoculata Hammer 1953b: 29	AK	-	NT	-	-	-	-	-	-	-	-	-	-	
A. granaria (Nicolet) 1847: 387	AK	-	NT	-	-	-	-	ON	QC	-	-	-	-	
A. hammerae Christiansen 1952: 135	AK	-	NT	-	-	-	-	-	-	-	-	-	-	
A. interior Fjellberg 1985a: 89	AK	-	-	-	-	-	-	-	-	-	-	-	-	
A. maritima (Guérin-Méneville) 1838: 11	-	-	-	BC	-	-	-	-	-	-	-	-	-	
A. martynovae Fjellberg 1985a: 96	AK	-	-	-	-	-	-	-	-	-	-	-	-	
A. narli Fjellberg 1985a: 105	AK	-	-	-	-	-	-	-	-	-	-	-	-	

A. papillosa (Axelson) 1902: 103	AK	-	-	-	-	-	-	-	-	-	-	-	-
A. papillosoides (Hammer) 1953b: 28	AK	-	NT	-	-	-	-	-	-	-	-	-	-
A. polaris (Hammer) 1954: 9	AK	-	-	BC	-	-	-	-	-	-	-	-	-
A. reducta Fjellberg 1985a: 102	AK	-	-	-	-	-	-	-	-	-	-	-	-
A. similis Fjellberg 1985a: 98	AK	-	-	-	-	-	-	-	-	-	-	-	-
A. subarctica Fjellberg 1985a: 94	AK	-	-	-	-	-	-	-	-	-	-	-	-
A. tullbergi Schött 1891b: 192	AK	-	NT	-	-	-	MB	ON	-	-	-	-	-
A. weberi Christiansen & Bellinger 1980-1981: 335	AK	-	NT	-	-	-	-	-	-	-	-	-	-
Genus *MICRANURIDA* Börner 1901a: 702													
M. porcella (Fjellberg) 1985a: 84	AK	-	-	-	-	-	-	-	-	-	-	-	-
M. pygmaea Börner 1901a: 702	AK	-	NT	BC	AB	-	MB	ON	QC	-	-	-	-
M. spirillifera (Hammer) 1953b: 25	AK	-	NT	BC	-	-	MB	-	QC	-	-	-	-
M. valiana (Fjellberg) 1985a: 82	AK	-	-	-	-	-	-	-	-	-	-	-	-
Subfamily Neanurinae													
Genus *CRISTOBELLA* Fjellberg 1985a: 116													
C. ornata (Folsom) 1902a: 89	AK	-	-	-	-	-	-	-	-	-	-	-	-
Genus *MORULINA* Börner 1906: 167													
M. gigantea (Tullberg) 1876: 41	AK	-	NT	-	-	-	-	-	-	-	-	-	-
M. kotzebuensis Bödvarsson 1960: 48	AK	-	-	-	-	-	-	-	-	-	-	-	-
M. mackenziana Hammer 1953b: 50	AK	-	NT	-	-	-	-	-	-	-	-	-	-
M. multatuberculata (Coleman) 1941: 7	-	-	-	BC	-	-	-	-	-	-	-	-	-
M. thulensis Hammer 1953b: 31	AK	YT	NT	-	-	-	MB	-	-	-	-	-	-
Genus *MORULODES* Cassagnau 1955: 160													
M. serratus (Folsom) 1916: 511	AK	-	-	BC	-	-	-	-	-	-	-	-	-
Genus *NEANURA* MacGillivray 1893b: 314													
Subgenus *Crossodonthina* Yosii 1954b: 791													
N. aleuta (Bödvarsson) 1960: 46	AK	-	-	-	-	-	-	-	-	-	-	-	-
N. prima (Bödvarsson) 1960: 43	AK	-	-	-	-	-	-	-	-	-	-	-	-
Subgenus *Deutonura* Cassagnau 1979: 192													
N. frigida Yosii 1969: 537	AK	YT	-	-	-	-	-	-	-	-	-	-	-
Subgenus *Endonura* Cassagnau 1979: 192													
N. tundricola Fjellberg 1985a: 120	AK	-	-	-	-	-	-	-	-	-	-	-	-
Subgenus *Lathriopyga* Caroli 1910: 321													
N. ornata Folsom 1902a: 89	AK	-	-	BC	-	-	-	-	-	-	-	-	-

N. setosa Canby 1926: 41	-	-	-	BC	-	-	-	-	-	-	-	-	-
Subgenus *Neanura* (s. str.)													
N. bara Christiansen & Bellinger 1980-1981: 373	-	-	-	-	-	-	-	-	QC	-	-	-	-
N. barberi (Handschin) 1928: 537	AK	-	-	-	-	-	-	ON	-	-	-	-	-
N. muscorum (Templeton) 1835: 97	-	-	NT	-	AB	-	MB	ON	QC	-	NS	-	NF
N. persimilis Mills 1934: 30	-	-	-	BC	-	-	-	-	-	-	NS	-	-
Genus *PARANURA* Axelson 1902: 102													
P. caeca Folsom 1916: 507	-	-	-	-	-	-	-	ON	QC	-	-	-	-
P. colorata Mills 1934: 28	AK	-	-	BC	-	-	-	-	-	-	-	-	-
P. quadrilobata Hammer 1953b: 24	AK	-	NT	-	-	-	-	-	-	-	-	-	-
P. sexpunctata Axelson 1902: 102	AK	-	-	-	-	-	-	ON	-	-	-	-	-
P. sitchensis Fjellberg 1985a: 110	AK	-	-	BC	-	-	-	-	-	-	-	-	-
Genus *PRATANURIDA* Rusek 1973: 187													
P. foxi Fjellberg 1985a: 78	AK	-	-	BC	-	-	-	-	-	-	-	-	-
P. tananensis Fjellberg 1985a: 76	AK	-	-	-	-	-	-	-	-	-	-	-	-

FAMILY ONYCHIURIDAE
Subfamily Onychiurinae

Genus *MULTIVESICULA* Rusek 1982: 33													
M. columbica Rusek 1982: 33	-	-	-	BC	-	-	-	-	-	-	-	-	-
M. dolomitica Rusek 1982: 39	-	-	NT	-	-	-	-	-	-	-	-	-	-
M. puctata Rusek 1982: 36	-	-	-	BC	-	-	-	-	-	-	-	-	-
Genus *ONYCHIURUS* Gervais 1841: 372													
Subgenus *Archaphorura* Bagnall 1949: 509													
O. absoloni (Börner) 1901b: 422	AK	-	NT	BC	AB	-	MB	-	QC	-	-	-	-
O. groenlandicus (Tullberg) 1876: 41	AK	-	NT	-	-	-	MB	-	-	-	-	-	-
O. nudus Fjellberg 1987: 283	AK	YT	-	-	-	-	-	-	-	-	-	-	-
O. pingicolus Fjellberg 1987: 285	AK	-	-	-	-	-	-	-	-	-	-	-	-
O. reversus Fjellberg 1987: 287	AK	YT	-	-	-	-	-	-	-	-	-	-	-
O. ursi Fjellberg 1984: 71	AK	-	-	-	-	-	-	-	-	-	-	-	-
Subgenus *Onychiurus* (s. str.)													
O. dentatus (Folsom) 1902c: 91	AK	-	-	BC	-	-	-	-	-	-	-	-	-
O. eisi Rusek 1976: 36	-	-	-	BC	-	-	-	-	-	-	-	-	-
O. eous Christiansen & Bellinger 1980-1981: 449	-	-	-	BC	-	-	-	-	-	-	-	-	-
O. flavescens Kinoshita 1916: 458	AK	-	NT	BC	-	-	MB	-	-	-	-	-	-
O. ramosus Folsom 1917: 648	AK	-	NT	BC	AB	-	-	ON	-	-	-	-	-

Genus *PROTAPHORURA* Absolon 1901b: 387

P. armatus (Tullberg) 1869: 15	AK	-	NT	-	-	-	-	ON	QC	-	NS	-	-
P. churchilliana (Hammer) 1953b: 44	-	-	-	-	-	-	MB	-	-	-	-	-	-
P. cocklei (Folsom) 1908: 200	AK	-	-	BC	-	-	-	-	-	-	-	-	-
P. debilis (Moniez) 1889: 31	AK	-	NT	-	-	-	-	-	-	-	-	-	-
P. decimpunctatus (Folsom) 1919: 6A	AK	-	NT	-	-	-	-	-	-	-	-	-	-
P. duodecimpunctatus (Folsom) 1919: 6	AK	-	NT	BC	-	-	-	-	-	-	-	-	-
P. macrodentatus (Hammer) 1953b: 43	-	-	NT	-	-	-	-	-	-	-	-	-	-
P. paucisetosus (Hammer) 1953b: 42	-	-	NT	-	-	-	-	-	-	-	-	-	-
P. pseudarmatus (Folsom) 1917: 646	AK	-	NT	BC	-	-	MB	-	-	-	-	-	-
P. sibiricus (Tullberg) 1876: 40	AK	-	NT	-	-	-	-	-	-	-	-	-	-
P. similis (Folsom) 1917: 640	-	-	-	-	-	-	-	-	QC	-	-	-	-
P. subtenuis (Folsom) 1917: 642	AK	-	NT	BC	AB	-	MB	ON	QC	-	-	-	-
P. uenoi (Yosii) 1954a: 62	AK	-	-	BC	-	-	-	-	-	-	-	-	-

Genus *LOPHOGNATHELLA* Börner 1908: 67

L. choreutes Börner 1908: 67	-	-	-	BC	-	-	-	-	-	-	-	-	-

Genus *SENSIPHORURA* Rusek 1976: 19

S. marshalli Rusek 1976: 21	-	-	-	BC	-	-	-	-	-	-	-	-	-

Subfamily Tullberginae

Genus *TULLBERGIA* Lubbock 1876: 324

Subgenus *Tullbergia* (s. str.)

T. arctica Wahlgren 1900: 359	AK	-	-	-	-	-	-	-	-	-	-	-	-
T. clavata Mills 1934: 38	-	-	-	-	-	-	-	-	QC	-	-	-	-
T. collis (Bacon) 1914: 84	-	-	NT	-	-	-	-	-	QC	-	-	-	-
T. falca Christiansen & Bellinger 1980-1981: 490	-	-	-	-	-	-	-	ON	-	-	-	-	-
T. granulata Mills 1934: 37	-	-	-	-	-	-	MB	ON	QC	-	-	-	-
T. iowensis Mills 1932: 264	-	-	NT	-	AB	-	MB	-	-	-	NS	-	-
T. krausbaueri Börner 1901c: 2	-	-	NT	-	AB	-	-	-	QC	-	-	-	-
T. macrochaeta Rusek 1976: 33	-	-	-	BC	AB	-	-	-	-	-	-	-	-
T. mala Christiansen & Bellinger 1980-1981: 500	-	-	-	-	-	AB	-	-	-	-	-	-	-
T. obtusochaeta (Rusek) 1976: 24	-	-	-	BC	-	-	-	-	-	-	-	-	-
T. pacifica (Rusek) 1976: 30	-	-	-	BC	-	-	-	-	-	-	-	-	-
T. ruseki Christiansen & Bellinger 1980-1981: 507	-	-	-	BC	-	-	-	-	-	-	-	-	-
T. simplex Gisin 1958: 89	AK	-	NT	-	-	-	-	-	-	-	-	-	-
T. vancouverica (Rusek) 1976: 27	-	-	-	BC	-	-	-	-	-	-	-	-	-
T. yosiii Rusek 1967: 191	AK	-	-	BC	-	-	-	-	-	-	-	-	-

FAMILY ISOTOMIDAE
Subfamily Anurophorinae

Genus *AGRENIA* Börner 1906: 171													
A. agilis Fjellberg 1986b: 101	-	-	-	BC	-	-	-	-	-	-	-	-	-
A. atroviridis Fjellberg 1986b: 104	-	-	-	BC	-	-	-	-	-	-	-	-	-
A. bidenticulata (Tullberg) 1876: 35	-	YT	NT	BC	AB	-	-	-	-	-	-	-	-
A. cyanura Fjellberg 1986b: 102	-	-	-	BC	AB	-	-	-	-	-	-	-	-
A. polymorpha Fjellberg 1986b: 96	-	-	-	-	AB	-	-	-	-	-	-	-	-
A. riparia Fjellberg 1986b: 103	AK	-	-	BC	-	-	-	-	-	-	-	-	-
Genus *ANUROPHORUS* Nicolet 1842: 52													
Subgenus *Anurophorus* (s. str.)													
A. septentrionalis Palissa 1966: 50	AK	-	NT	BC	-	-	MB	ON	-	-	NS	-	-
Genus *COLOBURELLA* Latzel 1918: 238													
Subgenus *Coloburella* (s. str.)													
C. octogenaria (Mills & Schmidt) 1957: 368	-	-	-	BC	-	-	-	-	-	-	-	-	-
Genus *PSEUDANUROPHORUS* Stach 1922a: 10													
P. arctica (Christiansen) 1952: 131	AK	-	-	-	-	-	-	-	-	-	-	-	-
Genus *ISOTOMODES* Linnaniemi 1907: 134													
I. productus (Axelson) 1903: 6	-	-	-	-	AB	-	-	ON	-	-	-	-	-
I. trisetosus Denis 1923: 243	-	-	-	-	-	-	-	-	QC	-	-	-	-
Genus *FOLSOMIDES* Stach 1922b: 117													
F. americanus Denis 1931: 126	-	-	NT	-	AB	-	MB	-	-	-	-	-	-
Genus *PROISOTOMA* Börner 1903: 172													
Subgenus *Proisotoma* (s. str.)													
P. beta Christiansen & Bellinger 1980-1981: 566	-	-	-	BC	-	-	-	-	-	-	-	-	-
P. immersa (Folsom) 1924: 1	-	-	-	BC	-	-	-	-	-	-	-	-	-
P. mackenziana Hammer 1953b: 56	AK	-	-	BC	-	-	-	-	-	-	-	-	-
P. minima (Absolon) 1901c: 33	-	-	-	-	-	-	-	ON	QC	-	-	-	-
P. minuta (Tullberg) 1871: 152	-	-	-	-	AB	-	MB	ON	-	NB	-	-	-
Genus *BALLISTURA* Börner 1906: 152													
B. crassicauda (Tullberg) 1871: 152	AK	-	-	-	-	-	-	-	-	-	-	-	-
B. ewingi (James) 1933: 99	-	-	-	-	-	-	-	ON	-	-	-	-	-
B. extra (Christiansen & Bellinger) 1980-1981: 586	AK	-	-	-	-	-	-	-	-	-	-	-	-
B. libra Christiansen & Bellinger 1980-1981: 588	-	-	-	BC	-	-	-	-	-	-	-	-	-
B. muskegis (Guthrie) 1903: 72	-	-	-	-	AB	-	-	ON	-	-	-	-	-

B. tuberculata (Stach) 1947: 218	-	-	-	-	-	-	-	-	-	-	NS	-	-	
Genus *APPENDISOTOMA* Stach 1947: 13														
A. bulbosa Folsom 1937b: 58	-	-	-	-	-	-	-	ON	-	-	-	-	-	
A. vesiculata (Folsom) 1937b: 57	-	-	-	-	-	-	-	ON	-	-	-	-	-	
Genus *ARCHISOTOMA* Linnaniemi 1912: 118														
A. besselsi (Packard) 1877: 52	AK	-	NT	-	-	-	MB	-	QC	-	-	-	-	
A. polaris Fjellberg & Poinsot 1975: 109	-	-	NT	-	-	-	-	-	-	-	-	-	-	
Genus *BLISSIA* Rusek 1985: 2077														
B. glabra Rusek 1985: 2079	-	-	NT	-	-	-	-	-	-	-	-	-	-	
Genus *CRYPTOPYGUS* Willem 1902a: 11														
C. arcticus Christiansen & Bellinger 1980-1981: 614	AK	-	-	-	-	-	-	-	-	-	-	-	-	
C. coeruleogriseus (Hammer) 1938: 43	AK	-	NT	-	-	-	-	-	-	-	-	-	-	
C. similis (James) 1933: 99	-	-	-	-	-	-	-	ON	-	-	-	-	-	
C. thermophila (Axelson) 1900: 113	-	-	-	-	-	-	-	-	QC	-	-	-	-	
Genus *FOLSOMIA* Willem 1902b: 280														
F. agrelli Gisin 1944: 154	-	-	NT	-	-	-	-	-	-	-	-	-	-	
F. alpha Christiansen & Tucker 1977: 371	AK	-	-	-	-	-	-	-	-	-	-	-	-	
F. bisetosa Gisin 1953: 233	-	-	NT	-	-	-	-	-	-	-	-	-	-	
F. candida Willem 1902b: 280	-	-	-	BC	-	-	-	ON	QC	-	-	-	-	
F. diplophthalma (Axelson) 1902: 106	AK	-	NT	-	-	-	MB	-	-	-	-	-	-	
F. duodecimoculata Ford 1962: 130	-	-	-	BC	-	-	-	-	-	-	-	-	-	
F. elongata (MacGillivray) 1896: 49	-	-	NT	-	AB	-	MB	ON	-	-	-	-	-	
F. fimetaria (Linné) 1758: 609	AK	-	NT	BC	AB	-	MB	ON	-	NB	-	-	NF	
F. gracilis (Stach) 1962: 11	AK	-	NT	-	-	-	-	-	-	-	-	-	-	
F. microchaeta Agrell 1939: 5	-	-	NT	-	-	-	-	-	-	-	-	-	-	
F. nivalis (Packard) 1873: 31	AK	-	NT	BC	AB	-	MB	-	QC	-	NS	-	-	
F. ozeana Yosii 1954b: 801	AK	-	-	-	-	-	-	-	-	-	-	-	-	
F. penicula Bagnall 1939: 57	-	-	-	-	-	-	-	ON	-	-	-	-	NF	
F. quadrioculata (Tullberg) 1871: 152	AK	-	NT	-	AB	SK	MB	ON	QC	NB	-	-	NF	
F. regularis Hammer 1953a: 4	AK	-	NT	-	-	-	-	-	-	-	-	-	-	
F. sensibilis Kseneman 1934: 3	AK	-	-	-	-	-	-	-	QC	-	-	-	-	
F. sexoculata (Tullberg) 1871: 152	AK	-	-	-	-	-	MB	-	-	-	-	-	-	
F. similis Bagnall 1939: 56	-	-	-	-	-	-	-	-	QC	-	-	-	-	
F. stella Christiansen & Tucker 1977: 379	AK	-	NT	BC	-	-	-	-	-	-	-	-	-	

F. taimyrica Martynova *et al.* 1973: 93	AK	-	-	-	-	-	-	-	-	-	-	-	-		
Subfamily Isotominae															
Genus *ISOTOMA* Bourlet 1839: 401															
Subgenus *Desoria* Nicolet 1841: 384															
I. agrelli Delamare 1950: 43	AK	-	-	BC	-	-	-	-	-	-	-	-	-		
I. alaskensis Fjellberg 1978: 94	AK	-	-	BC	-	-	-	-	-	-	-	-	-		
I. albella Packard 1873: 32	-	-	-	-	-	-	MB	ON	-	-	-	-	-		
I. atkasukiensis Fjellberg 1978: 95	AK	-	-	-	-	-	-	-	-	-	-	-	-		
I. blufusata Fjellberg 1978: 97	AK	-	-	-	-	-	MB	-	-	-	-	-	-		
I. canadensis Brown 1932: 334	-	-	NT	-	-	-	-	-	-	-	-	-	-		
I. creli Fjellberg 1978: 99	AK	-	-	-	-	-	-	-	-	-	-	-	-		
I. ekmani Fjellberg 1977: 9	AK	-	NT	BC	AB	-	-	ON	-	-	-	-	-		
I. fennica (Reuter) 1895: 27	-	-	-	-	-	-	MB	-	-	-	-	-	-		
I. flora Christiansen & Bellinger 1980-1981: 727	-	-	-	BC	-	-	-	-	-	-	-	-	-		
I. hiemalis Schött 1893: 70	AK	-	-	-	-	-	-	-	-	-	-	-	-		
I. inupikella Fjellberg 1978: 99	AK	-	-	-	-	-	-	-	-	-	-	-	-		
I. komarkovae Fjellberg 1978: 101	AK	-	-	-	-	-	-	-	-	-	-	-	-		
I. macleani Fjellberg 1978: 102	AK	-	-	-	-	-	-	-	-	-	-	-	-		
I. manitobae Fjellberg 1978: 103	-	-	-	-	-	-	MB	-	-	-	-	-	-		
I. multisetis Carpenter & Phillips 1922: 16	-	-	-	BC	-	-	-	-	-	-	-	-	NF		
I. nanseni Fjellberg 1978: 105	AK	-	-	-	-	-	-	-	-	-	-	-	-		
I. neglecta Schäffer 1900: 258	AK	YT	NT	-	-	-	-	ON	-	-	-	-	-		
I. nigra MacGillivray 1896: 56	-	-	-	-	-	-	-	ON	-	-	-	-	-		
I. nigrifrons Folsom 1937b: 105	-	-	-	-	-	-	-	ON	-	-	-	-	-		
I. notabilis Schäffer 1896: 187	AK	YT	NT	BC	AB	-	MB	ON	QC	-	NS	-	-		
I. quadra Christiansen & Bellinger 1980-1981: 747	-	-	-	-	-	-	MB	-	-	-	-	-	-		
I. taigicola Fjellberg 1978: 108	AK	-	-	-	-	-	-	-	-	-	-	-	-		
I. tariva Wray 1953b: 54	-	-	-	BC	-	-	-	-	-	-	-	-	-		
I. tigrina (Nicolet) 1842: 59	AK	-	NT	-	-	-	MB	ON	QC	-	-	-	-		
I. trispinata MacGillivray 1896: 51	-	-	-	BC	-	-	-	-	-	-	NS	-	-		
I. uniens Christiansen & Bellinger 1980-1981: 760	-	-	-	BC	-	-	-	-	-	-	-	-	-		
Subgenus *Isotoma* (s. str.)															
I. carpenteri Börner 1909: 109	-	-	-	-	-	-	-	-	QC	-	-	-	-		
I. sphagneticola Linnaniemi 1912: 171	AK	-	NT	-	-	-	-	-	-	-	-	-	-		
I. subviridis Folsom 1937b: 115	-	-	-	-	-	-	MB	ON	-	-	-	-	-		
I. violacea Tullberg 1876: 36	AK	-	NT	-	AB	-	MB	ON	-	-	-	-	-		
I. viridis Bourlet 1839: 401	AK	-	NT	BC	AB	-	MB	ON	QC	-	-	-	-		

Subgenus *Myopia* Christiansen & Bellinger 1980-1981: 768															
I. alaskana Christiansen & Bellinger 1980-1981: 769	AK	-	-	-	-	-	-	-	-	-	-	-	-	-	
Subgenus *Pseudisotoma* Handschin 1924: 111															
I. monochaeta Kos 1942: 125	-	-	-	BC	-	-	-	-	-	-	-	-	-		
I. sensibilis (Tullberg) 1876: 36	AK	-	NT	BC	-	-	-	ON	QC	-	-	-	-		
Subgenus *Vertagopus* Börner 1906: 171															
I. alpa Christiansen & Bellinger 1980-1981:775	-	-	-	BC	-	-	-	-	-	-	-	-	-		
I. arborea (Linné) 1758: 609	-	-	NT	BC	-	-	-	ON	-	-	-	-	-		
I. brevicauda (Carpenter) 1900: 274	-	-	NT	-	-	-	-	-	-	-	-	-	-		
I. pseudocinerea (Fjellberg) 1975: 212	-	-	-	-	-	-	-	ON	-	NB	-	-	-		
Genus *ISOTOMIELLA* Bagnall 1939: 59															
I. minor (Schäffer) 1896: 182	-	-	NT	-	AB	-	-	-	QC	-	-	-	-		
Genus *ISOTOMURUS* Börner 1903: 171															
Subgenus *Isotomurus* (s. str.)															
I. palustris (Müller) 1776: 184	AK	-	NT	BC	-	-	MB	ON	QC	-	NS	-	-		
I. palustroides Folsom 1937b: 77	AK	-	-	-	-	-	MB	ON	-	-	NS	-	-		
I. tricolor (Packard) 1873: 34	-	-	-	-	-	-	-	ON	-	-	-	-	-		
Genus *HYDROISOTOMA* Stach 1947: 15															
H. schaefferi (Krausbauer) 1898: 502	-	-	-	-	-	-	-	-	-	-	NS	-	-		
Genus *METISOTOMA* Maynard 1951: 94															
M. grandiceps (Reuter) 1891: 229	AK	-	NT	BC	AB	-	-	ON	QC	-	-	-	-		
Genus *MICRISOTOMA* Bellinger 1952: 20															
M. achromata Bellinger 1952: 20	-	-	-	BC	-	-	-	-	QC	-	-	-	-		
Genus *SEMICERURA* Maynard 1951: 99															
S. multispinata (James) 1933: 111	-	-	-	-	-	-	-	ON	-	-	-	-	-		
Genus *STACHANOREMA* Wray 1957: 108															
S. arnaudi Wray 1957: 108	-	-	NT	-	-	-	-	-	-	-	-	-	-		
Genus *TETRACANTHELLA* Schött 1891b: 191															
T. arctica Cassagnau 1960: 234	AK	-	NT	-	-	-	-	-	-	-	NS	-	-		
T. pacifica Rusek & Marshall 1976: 759	-	-	-	BC	-	-	-	-	-	-	-	-	-		
T. pilosa Schött 1891b: 192	-	-	NT	-	-	-	-	-	-	-	-	-	-		
Genus *UZELIA* Absolon 1901a: 209															

U. hansoni Mills & Richards 1953: 55	AK	-	NT	-	-	-	-	-	-	-	-	-	-	-
U. setifera Absolon 1901a: 210	-	-	-	-	-	-	-	-	-	-	NS	-	-	
Genus *WEBERACANTHA* Christiansen 1951: 24														
W. octa Christiansen 1951: 25	AK	-	NT	-	-	-	-	-	-	-	-	-	-	

FAMILY ENTOMOBRYIDAE

Subfamily Orchesellinae

Genus *ORCHESELLA* Templeton 1835: 92														
O. ainsliei Folsom 1924: 6	-	-	-	-	-	-	MB	ON	-	-	-	-	NF	
O. albosa Guthrie 1903: 61	-	-	-	-	-	-	-	ON	-	-	-	-	-	
O. cincta (Linné) 1758: 609	-	-	NT	BC	-	-	MB	ON	-	-	NS	-	NF	
O. folsomi Maynard 1933: 102	-	-	-	-	-	-	-	ON	-	-	-	-	-	
O. hexfasciata Harvey 1895: 196	-	-	-	-	-	-	-	ON	-	-	NS	-	-	
O. manitobae Mari Mutt 1985: 50	-	-	-	-	-	-	MB	-	-	-	-	-	-	
O. zebra Guthrie 1903: 61	-	-	-	BC	-	-	-	-	-	-	-	-	-	
Genus *HETEROMURUS* Wankel 1860: 203														
H. nitidus (Templeton) 1835: 94	-	-	-	-	-	-	-	ON	-	-	NS	-	-	

Subfamily Entomobryinae

Genus *CORYNOTHRIX* Tullberg 1876: 33														
C. borealis Tullberg 1876: 34	AK	-	NT	-	-	-	-	-	-	-	-	-	-	
Genus *ENTOMOBRYA* Rondani 1861: 40														
Subgenus *Entomobrya* (s. str.)														
E. assuta Folsom 1924: 6	-	-	-	BC	-	-	-	ON	QC	-	-	-	-	
E. atrocincta Schött 1896: 181	-	-	-	-	-	-	-	ON	-	-	-	-	-	
E. clitellaria Guthrie 1903: 75	-	-	-	-	-	-	-	ON	QC	-	-	-	-	
E. comparata Folsom 1919: 13a	AK	-	NT	-	AB	-	-	-	-	-	-	-	-	
E. confusa Christiansen 1958: 494	-	-	-	BC	AB	-	MB	ON	-	-	-	-	-	
E. decemfasciata (Packard) 1873: 40	-	-	-	-	-	-	-	ON	-	-	-	-	-	
E. erratica Brown 1932: 336	AK	-	NT	-	-	-	-	-	QC	-	-	-	-	
E. gisini Christiansen 1958: 502	-	-	-	-	AB	-	MB	-	-	-	-	-	-	
E. griseoolivata (Packard) 1873: 39	-	-	-	-	AB	-	-	ON	-	-	-	-	-	
E. intermedia Brook 1883: 274	-	-	-	-	-	-	-	ON	-	-	-	-	-	
E. kincaidi Folsom 1902a: 96	AK	-	-	-	-	-	-	-	QC	-	-	-	-	
E. multifasciata (Tullberg) 1871: 148	-	-	-	BC	-	-	-	ON	-	-	-	-	NF	
E. nivalis (Linné) 1758: 609	-	-	-	-	AB	-	MB	ON	-	-	-	-	-	
E. quadrilineata Bueker 1939: 15	-	-	NT	-	-	-	-	-	-	-	-	-	-	
E. triangularis Schött 1896: 182	-	-	-	BC	-	-	-	-	-	-	-	-	-	

Subgenus *Entomobryoides* Maynard 1951: 161														
E. dissimilis (Moniez) 1894: 207	-	-	-	-	-	-	-	ON	-	-	-	-	-	
E. guthriei Mills 1931: 4	-	-	-	BC	AB	-	-	-	-	-	-	-	-	
E. purpurascens (Packard) 1873: 39	-	-	-	-	AB	-	MB	ON	QC	-	-	-	-	
Genus *LEPIDOCYRTUS* Bourlet 1839: 391														
L. candida Folsom 1902b: 363	-	-	NT	-	-	-	-	-	-	-	-	-	-	
L. cinereus Folsom 1924: 9	-	-	-	-	AB	-	-	-	-	-	-	-	-	
L. curvicollis Bourlet 1839: 392	-	-	-	-	-	-	-	ON	-	-	-	-	-	
L. cyaneus Tullberg 1871: 150	AK	-	NT	BC	-	-	MB	ON	-	-	NS	-	-	
L. hirtus Christiansen & Bellinger 1980-1981: 947	AK	-	-	-	-	-	-	-	-	-	-	-	-	
L. lignorum (Fabricius) 1775: 302	-	-	-	-	-	-	-	ON	-	-	-	-	-	
L. paradoxas Uzel 1891: 50	-	-	-	-	-	-	-	-	QC	-	-	-	-	
L. unifasciatus James 1933: 107	-	-	-	-	-	-	-	ON	-	-	-	-	-	
L. violaceus Fourcroy 1785: 525	-	-	NT	-	-	-	MB	-	-	-	-	-	-	
Genus *PSEUDOSINELLA* Schäffer 1897: 38														
P. alba (Packard) 1873: 37	-	-	-	BC	-	-	-	ON	QC	-	NS	-	-	
P. collina Wray 1952: 104	-	-	-	BC	-	-	-	-	-	-	-	-	-	
P. octopunctata Börner 1901a: 705	-	-	-	-	AB	-	-	-	-	-	-	-	-	
P. violenta (Folsom) 1924: 10	-	-	-	-	-	-	MB	ON	QC	-	-	-	-	
Genus *SEIRA* Lubbock 1870: 279														
S. bipunctata Packard 1873: 37	-	-	-	BC	-	-	-	-	-	-	-	-	-	
S. erudita Nicolet 1842: 74	-	-	NT	-	-	-	-	-	-	-	-	-	-	
Genus *SINELLA* Brook 1882: 541														
Subgenus *Caecobrya* Yosii 1956a: 622														
S. caeca (Schött) 1896: 178	-	-	-	-	-	-	-	ON	-	-	-	-	-	
Subgenus *Sinella* (s. str.)														
S. baca Christiansen & Bellinger 1980-1981: 898	-	-	-	BC	-	-	-	-	-	-	-	-	-	
S. binoculata (Schött) 1896: 178	-	-	-	BC	-	-	-	-	-	-	-	-	-	
S. curviseta Brook 1882: 544	-	-	-	BC	-	-	-	-	-	-	-	-	-	
Genus *WILLOWSIA* Shoebotham 1917: 431														
W. buskii (Lubbock) 1870: 280	AK	-	-	BC	AB	SK	MB	ON	QC	-	-	-	-	
W. nigromaculata (Lubbock) 1873: 146	-	-	-	-	-	-	-	ON	QC	-	-	-	NF	

FAMILY CYPHODERIDAE

Genus *CYPHODERUS* Nicolet 1842: 81														
C. similis Folsom 1927: 12	-	-	-	-	-	-	-	ON	-	-	-	-	-	

FAMILY TOMOCERIDAE

Genus *TOMOCERUS* Nicolet 1842: 67

Subgenus *Pogonognathellus* Paclt 1944: 92

T. bidentatus Folsom 1913: 463	-	-	-	-	-	-	MB	ON	-	-	-	-	-
T. dubius Christiansen 1965: 671	AK	-	-	BC	-	-	-	-	-	-	-	-	-
T. elongatus Maynard 1951: 126	AK	-	-	-	-	-	-	-	-	-	-	-	-
T. flavescens Tullberg 1871: 149	AK	-	NT	BC	AB	-	MB	ON	QC	-	NS	-	-

Subgenus *Plutomurus* Yosii 1956b: 78

T. brevimucromatus Denis 1929: 176	-	-	-	BC	-	-	-	-	-	-	-	-	-
T. wilkeyi Christiansen 1965: 659	-	-	-	BC	-	-	-	-	-	-	-	-	-

Subgenus *Tomocerina* Yosii 1956b: 78

T. lamelliferus Mills 1934: 84	-	-	-	BC	-	-	-	ON	-	-	-	-	-
T. minor (Lubbock) 1862: 598	-	-	-	BC	-	-	-	ON	-	-	NS	-	NF

Subgenus *Tomocerus* (s. str.)

T. vulgaris (Tullberg) 1871: 149	-	-	-	-	AB	-	-	ON	-	-	-	-	-

SUBORDER SYMPHYPLEONA

FAMILY SMINTHURIDIDAE
Subfamily Sminthurinae

Genus *SMINTHURIDES* Börner 1900: 616

Subgenus *Sminthurides* (s. str.)

S. annulicornis Axelson 1905: 793	-	-	-	-	-	-	-	ON	-	-	-	-	-
S. aquaticus (Bourlet) 1843: 146	AK	YT	NT	BC	-	-	-	ON	-	-	-	-	-
S. bifidus Mills 1934: 90	-	-	-	-	-	-	-	ON	-	-	-	-	-
S. lepus Mills 1934: 91	-	-	-	-	-	-	-	ON	-	-	-	-	-
S. macnamarai Folsom & Mills 1938: 258	-	-	-	-	-	-	-	ON	-	-	-	-	-
S. malmgreni (Tullberg) 1876: 30	AK	YT	NT	-	-	-	MB	ON	-	-	-	-	-
S. occultus Mills 1934: 91	-	-	NT	-	-	-	MB	ON	-	-	-	-	-

Subgenus *Stenacidia* Börner 1906: 182

S. violaceus (Reuter) 1881: 203	-	-	-	-	-	-	-	ON	-	-	-	-	-

Subgenus *Denisiella* Folsom & Mills 1938: 264

S. sexspinnatus Denis 1931: 156	-	-	-	BC	-	-	-	-	-	-	-	-	-

Genus *SPHAERIDIA* Linnaniemi 1912: 248

S. pumilis (Krausbauer) 1898: 495	AK	-	NT	BC	-	-	MB	-	-	-	-	-	-
S. serrata (Folsom & Mills) 1938: 268	-	-	-	BC	-	-	-	-	-	-	-	-	-

FAMILY ARRHOPALITIDAE

Genus *ARRHOPALITES* Börner 1906: 182

A. amarus Christiansen 1966: 62	-	-	-	-	-	-	-	ON	-	-	-	-	NF
A. benitus (Folsom) 1896a: 446	AK	-	-	BC	-	-	-	ON	-	-	-	-	-
A. caecus (Tullberg) 1871: 146	-	-	-	-	AB	-	-	-	-	-	-	-	-
A. clarus Christiansen 1966: 57	-	-	-	BC	-	-	-	-	-	-	-	-	-
A. hirtus Christiansen 1966: 61	AK	-	-	BC	-	-	-	-	QC	-	-	-	-
A. pygmaeus (Wankel) 1860: 203	AK	-	-	-	AB	-	-	ON	-	-	NS	-	-

FAMILY KATIANNIDAE

Genus *SMINTHURINUS* Börner 1901d: 99

Subgenus *Katiannina* Maynard 1951: 242

S. macgillivrayi (Banks) 1897: 34	-	-	-	-	-	-	-	ON	-	-	-	-	-

Subgenus *Polykatianna* Salmon 1946: 54

S. sminthurinus (Mills) 1934: 99	-	-	-	BC	-	-	-	-	-	-	-	-	-

Subgenus *Sminthurinus* (s. str.)

S. conchyliatus Snider 1978: 221	-	-	-	BC	-	-	-	-	-	-	-	-	-
S. elegans (Fitch) 1863: 657	AK	-	-	-	-	-	-	ON	QC	-	NS	-	-
S. henshawi (Folsom) 1896a: 449	-	-	-	-	-	-	-	ON	QC	-	-	-	-
S. quadrimaculatus (Ryder) 1879: 335	AK	-	NT	BC	-	-	-	-	QC	NB	-	-	-

FAMILY DICYRTOMIDAE

Genus *DICYRTOMA* Bourlet 1841: 41

Subgenus *Dicyrtoma* (s. str.)

D. flammea (Maynard) 1951: 281	-	-	-	-	-	-	-	ON	QC	-	-	-	-
D. fusca (Lubbock) 1873: 120	-	-	-	-	-	-	-	ON	-	-	NS	-	-
D. hageni (Folsom) 1896b: 344	-	-	-	-	-	-	-	ON	-	-	-	-	-

Genus *DICYRTOMINA* Börner 1903: 167

D. minuta (O. Fabricius) 1783: 307	-	-	-	-	-	-	-	-	-	-	NS	-	-

Genus *PTENOTHRIX* Börner 1906: 185

P. atra (Linné) 1758: 608	-	-	-	BC	-	-	MB	ON	QC	-	NS	-	-
P. maculosa (Schött) 1891a: 14	-	-	-	BC	-	-	-	ON	-	-	-	-	-
P. marmorata (Packard) 1873: 42	-	-	-	-	-	-	MB	ON	-	-	NS	-	-
P. palmata (Folsom) 1902a: 102	AK	-	-	-	-	-	-	-	-	-	-	-	-

FAMILY SMINTHURIDAE

Genus *SMINTHURUS* Latreille 1802: 71
Subgenus *Allacma* Börner 1906: 183
S. purpurescens (MacGillivray) 1894: 109 - - - - - - - - - - - - NF

Subgenus *Sminthurus* (s. str.)
S. incisus Snider 1978: 240 AK - - - - - - - - - - - -
S. medialis Mills 1934: 103 - - - - - - - ON - - - - -
S. mencenbergae Snider 1983: 115 - - - - AB - - - - - - - -
S. sylvestris Banks 1899: 195 - - - - - - - - QC - - - -
S. viridis (Linné) 1758: 608 AK - NT - - - - - - - - - -

Genus *SPHYROTHECA* Börner 1906: 183
S. minnesotensis (Guthrie) 1903: 52 - - - - - - - ON - - - - -

FAMILY BOURLETIELLIDAE

Genus *BOURLETIELLA* Banks 1899: 194
Subgenus *Bourletiella* (s. str.)
B. arvalis (Fitch) 1863: 673 - - - - - - - ON - - - - -
B. bilineatus (Bourlet) 1843: 146 - - NT - - - - - - - - - -
B. hortensis (Fitch) 1863: 668 - - - BC - - MB ON QC - NS - -

Subgenus *Heterosminthurus* Stach 1955: 53
B. aquatica Maynard 1951: 259 - YT NT - - - MB - - - - - -

Genus *PSEUDOBOURLETIELLA* Stach 1956 :134
P. spinata (MacGillivray) 1893a: 127 - YT - BC - - MB ON QC - NS - NF

Genus *DEUTEROSMINTHURUS* Börner 1901d: 104
D. undulatus Hammer 1953b: 59 - - NT - - - - - - - - - -

SUBORDER NEELIPLEONA

FAMILY NEELIDAE

Genus *NEELIDES* Caroli 1912: 1
N. minutus (Folsom) 1901b: 221 AK - - - - - - - - - - - -

Genus *MEGALOTHORAX* Willem 1900: 7
M. incertus Börner 1903: 160 - - - - - - - - QC - - - -
M. minimus Willem 1900: 7 AK - NT BC AB - - - QC - NS - -

Genus *MACKENZIELLA* Hammer 1953b: 60
M. psocoides Hammer 1953b: 60 - - NT - - - MB - - - - - - -

FOSSIL COLLEMBOLA

Cretaceaus amber from Manitoba

Genus *PROTENTOMOBRYA* Folsom 1937a: 15
P. walkeri Folsom 1937a: 17 - - - - - - MB - - - - - -

The following is a complete list of references relating to the Collembola fauna of Canada and Alaska. Not all of these are cited in the text. Those not cited contain only distributional data.

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NEW RECORDS OF DRYWOOD TERMITE INTRODUCTION, INTERCEPTION AND EXTIRPATION IN ONTARIO

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Four new instances of the introduction to Ontario of drywood termites, *Cryptotermes* spp. (Isoptera: Kalotermitidae), are reported. The first case involved an active structural infestation of *Cryptotermes brevis* (Walker) which was controlled by a combination of wood removal and the drill-and-injection technique. The second case also involved *C. brevis* but was limited to a piece of furniture which had been transported from Florida. The third and fourth cases involved the interception of wood crates brought in as air cargo from Malaysia which contained large colonies of both *Cryptotermes domesticus* (Haviland) and *Cryptotermes dudleyi* Banks.

Introduction

As a northern country, Canada historically has had few problems with termites, a largely tropical order of insects (Isoptera). However, two genera, *Zootermopsis* (Termopsidae) and *Reticulitermes* (Rhinotermitidae), do occur naturally in southern British Columbia (Vickery and Kevan 1983). During this century the eastern subterranean termite, *Reticulitermes flavipes* (Kollar), has been introduced into Ontario from the United States presumably on several different occasions as reflected by the numerous isolated infestations now known from 30 different municipalities in Ontario (Myles 1991). The establishment of *R. flavipes* in Winnipeg in 1987 (Anonymous 1989) demonstrates the ability of certain species to survive frigid northern winter conditions after gaining a successful toehold in the urban environment. While this has been repeatedly demonstrated in Canada by the subterranean termite, *R. flavipes* (Grace 1990; Myles and Grace 1991; Toronto Housing Department 1993; Vickery and Kevan 1983), we are now beginning to see more instances of the introduction and sometimes successful establishment of drywood termites (Kalotermitidae) (Vickery and Kevan 1983; Grace *et al.* 1991) as further documented by four additional cases described in this paper.

Case Descriptions

Case 1. Discovery of infestation. On 17 September 1990 a home owner brought an infested piece of cabinet wood from his house to the office of Mr. Geoff Cutten at the Ontario Ministry of the Environment. Mr. Cutten and I visited the house two days later in Malton, Mississauga. Apparently the initial infestation had established in the kitchen cabinets which had been recently removed. The most badly damaged cabinets had been set out on the curb and picked up by the

local garbage service two days earlier. Some less damaged cabinets were still in the backyard. These cabinets were salvaged and taken to my laboratory where the termites were extracted for identification and study.

Extent of infestation in house. The colony in the kitchen cabinets appeared to have been completely removed. However, we discovered a second site of infestation separate from the kitchen site. This second site was probably initiated by a pair of alates that flew from the kitchen colony. It seems likely that the cabinets would have been the original source of introduction. The second colony was in the floor of the first floor bathroom. The pellets from this colony had accumulated in piles on the ceiling panels below the bathroom in the finished basement. By removing and inspecting the ceiling panels, we mapped the position and extent of the infestation and found that it centred around the toilet and bath in the floor above. Two incipient colonies were also found which were evidently started in nail holes in the floor joists. We dug out both with a screwdriver and found only dead dealates. The possibility of additional points of infestation in other inaccessible parts of the house could not be discounted.

Species Identification. About 100 live termites were extracted from the salvaged cabinets including five soldiers. The soldiers enabled positive identification of the species as *Cryptotermes brevis* (Walker), the West Indian powderpost termite (Gay and Watson 1982). The alates on the basement ceiling panels also matched the description of *C. brevis* on the basis of wing venation, eye shape, mandible dentition, absence of arolium, and colour pattern. Later, two soldier head capsule fragments were also found among the pellets from the ceiling panels, thus confirming that both colonies were *C. brevis*. There were also numerous wings and dead, dry, and partly dermestid-eaten alates scattered about on the ceiling panels. *Cryptotermes brevis*, native to the West Indies and common in Florida, has previously been recorded in Canada and is reported as established at two sites in British Columbia (Vickery and Kevan 1983).

Estimation of colony size. The faecal pellets swept from the basement ceiling panels had a total weight of 29.6 grams. Based on laboratory measurements obtained over one month, *C. brevis* pseudergates generate 0.03 mg frass/day/termite at 26°C, 95% R.H. This represents 986,667 termite days. Assuming each termite takes two years to develop from egg to alate, this is a development time of 730 days and would represent a total population of 1,352 termites. This is a conservative estimate because it does not include the frass that remained inside the wood. A population this size in a drywood termite species would represent a colony about ten years old (Harvey 1934). Since a relatively high percentage of individuals transform into alates in drywood termite colonies (Myles 1988), it is likely that at least half of these developed into alates over the years, and flew within the house. This was supported by the observation of many corpses and wings and by the two dead incipient colonies mentioned above.

Control of the colony. Methyl bromide, the fumigant that had been used to control an infestation of drywood termites in Toronto in 1990 (Grace *et al.* 1991), was under review by Agriculture Canada and was not available for use in this case. It was therefore decided to take a two-pronged approach to control: 1) physical removal of the accessible infested boards and plywood flooring, and 2) injection of the termiticide, chlorpyrifos, using the Whitmire product, PT-270.

On 9 September 1992 the entire floor and plywood subfloor of the infested bathroom was physically removed by a contractor. No termites were found in the plywood although there was extensive damage and frass pellets were plentiful. The plywood floor boards had previously been sprayed with a pyrethroid based aerosol insecticide by the home owner. It is possible that the heavy spraying and the petroleum distillates in the spray had killed many of the termites in the plywood. Three of the ten foot 2" X 8" floor joists which showed evidence of infestation were physically removed. When later sawn up, two of these were found to have live termites.

Approximately 130 termites were counted including 30 alates, the queen, many eggs, and young larvae. The fact that the primary queen and eggs were collected indicates that the main pocket of the bathroom colony was mostly, if not entirely, removed.

On the same day all the remaining joists in the bathroom were drilled from the top and sides and chlorpyrifos injected into the drill holes. All the cut ends of the plywood floor and the 2" X 4" sill plates around the perimeter of the bathroom were also drilled and injected. All of the remaining floor joists that were accessible from the room below the bathroom were also drilled and treated. No new pellets have been reported since the treatment was performed and the colony is presumably eradicated.

Case 2. Infested furniture from Florida. On 2 October 1992, Mr. Al Pessoa, a housing inspector for the Toronto Housing Department, brought a sample of suspected drywood termite pellets to my lab for identification. The pellets had come from a corner hutch which had been brought to Toronto from Florida in 1989. I obtained the infested piece of furniture and with the permission of the owner dismantled the lower portion of it where the most severe damage was evident. Two plywood panels were split open revealing extensive damage to the wood. About 35 grams of faecal pellets were collected. Calculating in the same manner as above, this represents a lifetime population of the colony of at least 1,598 termites and a colony about ten years old. Dead corpses of about 30 termites were found including several soldiers. The species was identified as *C. brevis*. It was somewhat surprising to find all the termites dead. It is possible that the hutch became too dry from being placed near a heater during the winter. As observed in the previous case, dermestid beetle larvae were found feeding on the dead termites. The hutch was returned to the owner who was advised to keep it in the outdoor garage for the winter where freezing temperatures would surely kill any remaining live termites. No further action was taken.

Case 3. Air cargo from Malaysia. On 11 November 1994 a call was received from a company (name withheld) in Mississauga. The previous day the company had received an air cargo shipment from Malaysia through Pearson International Airport of which two crates appeared to be infested with termites. The crates were dismantled and brought to the laboratory for further examination. The boards were sawn into 1-2 cm slices on a band saw exposing the termite galleries. The termites and frass pellets were knocked out and collected. The debris with the termites and pellets was sorted through two sieves (Tyler No. 12 and No. 35). The coarse debris was discarded. The termites passed through the No. 12 sieve and were caught with medium debris on the No. 35 sieve. The frass pellets were cleanly sieved through the No. 35. About 1,000 ml (= 541 grams) of frass were collected. Using the defecation rate from above, this would represent a lifetime colony population of 25,046 termites and therefore a very large colony, perhaps over 20 years old.

Species identification and colony census. An entire mature colony of *Cryptotermes domesticus* (Haviland) appears to have been present in the crates as well as a small colony or part of a colony of *Cryptotermes dudleyi* Banks (Table I). *Cryptotermes domesticus* soldiers have a unique overhanging frontal flange and concave, receding frons, and prominent genal horns. The alates and primary reproductives are yellowish. *Cryptotermes dudleyi* is a larger species with the soldier head capsule longer than wide and with tawny brown alates (Gay and Watson 1982). Samples were sent to Dr. Leigh Miller, CSIRO, Canberra, Australia who confirmed the species identifications.

A total of 3,483 termites arrived alive in Canada. In addition, 41 fragments of soldier head capsules of *C. domesticus* and 14 fragments of soldier head capsules of *C. dudleyi* were picked

TABLE I. Census of termites intercepted on 11 November 1994 by species and caste.

Caste	Species		
	Cryptotermes domesticus	*Cryptotermes dudleyi*	mixed
primary male	1		
ergatoid female	1		
alates	31		
soldiers	20 + 41*	2 + 14*	
presoldiers	2		
long pad nymphs			1246
short pad nymphs			933
pseudergates			1076
larvae			159
eggs			12

* fragments of soldier head capsules

from the frass and debris. Although the termites were alive, many appeared moribund and it was presumed that this was due either to conditions experienced during air shipment or exposure to near freezing temperatures the night after their arrival.

Case 4. Air cargo from Malaysia. On 25 May 1995 another call was received from the same company as before to again report the presence of termites in crates from Malaysia. The infested dunnage was retrieved, consisting of several boards, wood blocks and old plywood. Although no effort was made to extract every termite, in two days two technicians were able to extract a total of 1,652 live termites including many healthy alates. Both *Cryptotermes domesticus* and *Cryptotermes dudleyi* were present. As before, only the alates and soldiers could be distinguished while the immature stages (larvae, pseudergates and nymphs) could not (Table II).

Pest status and potential danger of establishment. Both species intercepted from Malaysia are native to southeast Asia and both are often associated with structural timbers and wood furnishings (Peters 1982). Consequently, both species have frequently been transported through commerce and are therefore referred to as "tramp" species (Gay and Watson 1982). Both have been introduced and established in many countries outside their native ranges. *Cryptotermes domesticus* is now established in the following countries: Sri Lanka, India, Bangladesh, Indonesia, Philippines, Australia, Marshall Islands, Trinidad, Panama, Costa Rica, Cocos Island, Madagascar, Mauritius, Somalia, Uganda, Kenya, and Tanzania (Coaton and Sheasby 1979); and Cook Islands, French Polynesia, New Britain, Vanuatu (New Hebrides), Papua New Guinea, Samoa, Sabah, Singapore, and Soloman Islands (Gay and Watson 1982). *Cryptotermes dudleyi* has been introduced and established in Panama, Costa Rica, East Pakistan, India, Kenya, Tanzania, Somalia, and Australia and is questionably established also in Trinidad, Marshall Islands, Mauritius, Madagascar, and Cocos Island (Gay 1969). This report appears to be the first record of either species being intercepted in Canada (Vickery and Kevan 1983; Grace *et al.* 1991).

Voucher specimens. Voucher specimens of all three species have been deposited with the Entomology Department of the Royal Ontario Museum.

TABLE II. Census of termites intercepted on 25 May 1995 by species and caste.

Caste	Species		
	Cryptotermes domesticus	*Cryptotermes dudleyi*	mixed
soldiers	46	15	
alates	48	221	
long pad nymphs			627
short pad nymphs			588
pseudergates & larvae			107

Discussion

The cases of *Cryptotermes* introduction described above underscore the earlier conclusion of Gay (1969) that a number of species in this genus are frequently moved in commerce and warrant special attention. This transportability is evidently due to their unique ability to survive extremely dry conditions in structural wood, furniture, shipping crates, pallets, and other wooden articles. Over the past four years, new cases of drywood termites have been reported to the Urban Entomology Program, at the University of Toronto at the rate of one per year. With the large amount of air cargo and freight shipping typical of a commercial hub such as Toronto and the highly international character of the populace, it is perhaps not surprising that the rate of such introductions may be increasing. The first case described here as well as the earlier case reported by Grace *et al.* (1991) demonstrate that drywood termites are able to move from the original piece of wood in which they were introduced and establish successful structural infestations. So far, these known infestations have been extirpated before further spread has occurred. However, it is likely that many other cases have not been reported. Costly quarantine and eradication programs to control these termites after their introduction in other countries such as Australia (Wylie and Peters 1987) and South Africa (Coaton and Sheasby 1979) indicate that a greater level of awareness and vigilance is warranted in Canada. Customs inspectors should be particularly aware of the likelihood of drywood termites in wooden dunnage from tropical countries. Inspectors need to be familiar with the unique, diagnostic appearance of drywood termite faecal pellets (Figs. 1 & 2). These coarse, gritty pellets, spilled from infested wood, are the most likely visual evidence to be encountered.

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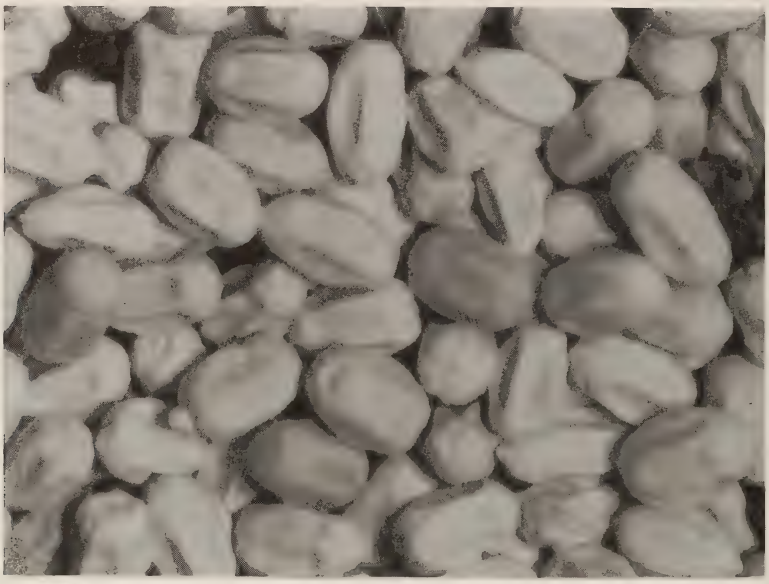

FIGURE 1. Faecal pellets of *Cryptotermes brevis*. Pellets are keg-shaped with a flattened end and a pointed end and hexagonal in cross section. Pellets are approximately 0.45 to 0.55 mm in width by 0.7 to 0.8 mm in length.

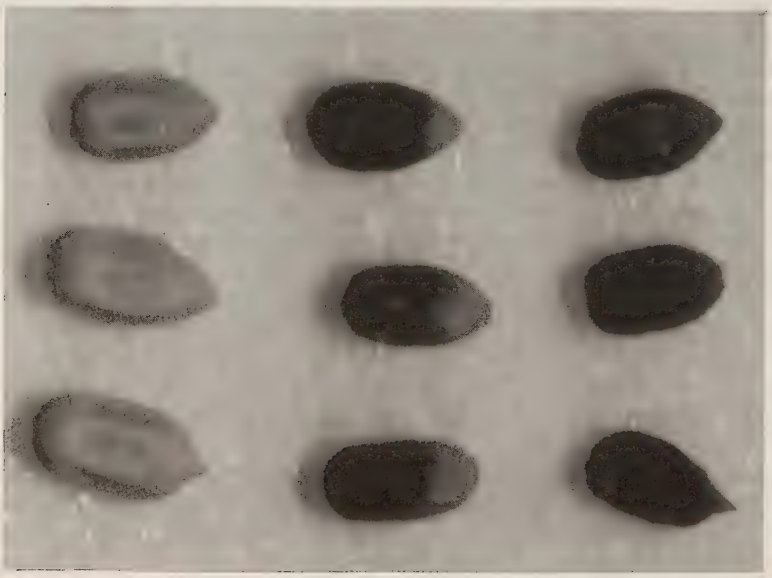

FIGURE 2. Most pellets are pulpy and light tan in colour (left side); some are partly composed of darker material, resin or lignin, (middle); and a few pellets are entirely composed of dark resin-like material (right side).

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EVALUATION OF INSECTICIDES FOR CONTROL OF THE RED PINE CONE BEETLE, *CONOPHTHORUS RESINOSAE* HOPKINS AND THE WHITE PINE CONE BEETLE, *C. CONIPERDA* (SCHWARZ)

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When solutions of fenitrothion, lindane, carbaryl, permethrin, azinphos-methyl or dimethoate were applied to the pronotum and elytra of individual *Conophthorus resinosae* Hopkins or *C. coniperda* (Schwarz) to determine their toxicity, azinphos-methyl was 5-20 times more toxic to both species than the other compounds. Similarly, in tree shoot residue tests, azinphos-methyl was among the most toxic insecticides to both species of beetles. Lindane was most toxic as a residue. With the exception of the topical application of carbaryl, there were no significant differences in the toxicities of the insecticides between *C. resinosae* and *C. coniperda* by either route of exposure. On the basis of the results, it appears that azinphos-methyl may provide effective control of both species of cone beetles in the field as a contact insecticide, with lindane better as a residue.

Introduction

Conophthorus resinosae and *C. coniperda* (Coleoptera: Scolytidae) are the most serious pests of red pine, *Pinus resinosa* Ait., and white pine, *P. strobus* L., seed cones, respectively. Each is capable of completely destroying a cone crop within 4-6 weeks (Hedlin *et al.* 1981). Cone beetle populations often remain high for several years (unpublished observations). In Ontario, red pine cone beetle, *C. resinosae* Hopkins and white pine cone beetle, *C. coniperda* (Schwarz) adults emerge from their overwintering sites in mid-May and fly to tree crowns to begin feeding on seed cones. They appear not to fly directly to cones, but alight randomly on branches and walk to cones (Mattson *et al.* 1984). Female beetles bore into the base of a cone and release a sex pheromone, pityol, to attract males (de Groot *et al.* 1991; Pierce *et al.* 1995). Brood development takes place inside the cone and young *C. coniperda* adults usually remain in the brood cone until the following spring. Thus, the adults are vulnerable to insecticides during foraging for brood sites and mating.

Laboratory bioassays have shown that several contact insecticides are effective against the mountain pine cone beetle, *C. ponderosae* Hopkins (Haverty and Wood 1981; Haverty and Dell 1984). In field tests, application of permethrin to tree crowns provided effective control (Shea *et*

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al. 1984). Herein we report the results of laboratory bioassays to determine the topical and the foliar residue toxicity of six insecticides to *C. resinosae* and *C. coniperda* selected on the basis they had been used in the past against beetle pests of trees or seed and cone insects in North America and Europe.

Materials and Methods

Insects. Adult beetles were collected in the late summer and early fall from red pine near Thessalon, Ontario, and white pine near Chalk River, Ontario. Infested shoots containing *C. resinosae* or cones infested with *C. coniperda* were placed in paper bags and held in darkness at 80% RH and 1°C for up to 4 months to satisfy overwintering requirements.

After removal from cold storage, infested cones and shoots were warmed at room temperature (1-2 d, at about 20°C) and then warmed under a 60W incandescent light to accelerate the emergence of beetles. Emerged beetles were placed in petri dishes lined with filter paper moistened with water and held for 1-2 d at 4°C until enough beetles were collected for each insecticide test. Before treatment, beetles were removed from cold storage and allowed to warm up at room temperature for 30-60 min after which they were selected at random, placed into groups of 5, and weighed.

Insecticides. Six insecticides were tested: 1) fenitrothion (Sumithion, 96% technical, Sumitomo Chemical Co.), 2) lindane (Lindane, 95% technical, Ciba Geigy), 3) carbaryl (Sevin, 99.9% technical, Union Carbide, now Rhône-Poulenc), 4) permethrin, (Ambush 500EC, Chipman Chemicals, now Zeneca), 5) azinphos-methyl (Guthion 94% technical, Mobay, now Bayer) and 6) dimethoate (Cygon, 97% technical, Cheminova). Concentrations of the insecticides were formulated on a weight/volume basis of the active ingredient in reagent grade acetone.

Topical Toxicity. A preliminary assessment of each insecticide was made to determine which range of concentrations from 0.0001 to 1.0% resulted in 0 to 100% mortality. From this assessment, six concentrations of each insecticide were evaluated further. Each concentration (treatment) was replicated three times on three groups of five insects (45 insects). Insecticides were applied to the pronotum and elytra of individual insects by a microapplicator (Tracor Atlas Inc., Houston, Texas) fitted with a Hamilton 10 μL syringe, calibrated to deliver 0.5 μL per application. Control insects were treated with acetone only or not treated. After treatment, insects were placed in groups of 5 in 9-cm petri dishes lined with filter paper. Petri dishes were vented to prevent a buildup of insecticide fumes and held at 21°C, 70% RH, and 16L:8D photoperiod. Insects were observed 1, 3 and 7 days after treatment to record the number of healthy, dead and moribund (almost dead) insects. Mortality was complete by the 7th day: data from the 1st and 3rd days were used to document the progression of mortality only and were not used in the analysis.

Toxicity of Tree Residues. To determine the toxicity of tree shoot residues of the insecticides, red pine and white pine shoots (stripped of their needles) were cut 5 cm long and dipped in the insecticide solutions for 5 seconds. Needles were stripped from the shoots to facilitate dipping and to simulate the surface conditions of the cones. Six concentrations of each insecticide were used. Dipped shoots were air-dried in a fume hood for 20 to 30 minutes. After being dried, two shoots were placed on moistened filter paper in a 9-cm vented petri dish containing five insects. For each insecticide concentration, three groups of five insects were tested, and repeated three times for a total of 45 insects. Mortality was recorded and assessed as above.

Data analyses. Dose-mortality data were analyzed by probits using the POLO program (Russell *et al.* 1977; Robertson *et al.* 1980). For each insecticide, LD_{50}, and LD_{95} values at day 7 were

calculated for topical applications, and LC_{50} and LC_{95} values calculated at 7 days for shoot deposits. Regression lines were compared using the likelihood ratio test (Robertson and Preisler 1992).

Results and Discussion

In topical applications, azinphos-methyl was five to twenty times more toxic to *C. resinosae* and *C. coniperda* than were the other compounds (Table I). In shoot residue tests, azinphos-methyl was again highly toxic, but lindane was more toxic for both insects (Table II). Although lindane was one of the most toxic to the beetles exposed to treated shoots, it was one of the least toxic when the insects were treated directly by topical application. Lindane is a persistent organochlorine compound that has a high degree of volatility and is used against borers in woody plants where the vapours can reach the insect (Ware 1980). The toxic vapours and persistence of lindane may have contributed to the high mortalities observed in our shoot tests. In contrast, permethrin was the least toxic on treated shoots but the second most toxic topically (Table II). However, the results from the assays to determine the effectiveness of permethrin residues should be viewed with caution. In the bioassays, it was noted that very little feeding occurred after the first 24 h and only a few beetles were observed on the foliage after this time. Over the 7-d observation period, beetles were lethargic and even moribund, in some cases. These observations were reflected in the probit model, which failed to generate a positive linear response in mortality with increased insecticide concentrations. A similar response to permethrin has been observed in the white pine weevil, *Pissodes strobi* (Peck), in both lab and field studies (de Groot and Helson 1993) and may be due to "rapid knockdown" or repellency. Although the toxicology tests based on mortality indicated a rather high LD_{95} for permethrin in the residue tests, its potential effectiveness is somewhat hidden as many of the beetles remaining were almost dead and had completely ceased feeding after 7 days. Observation indicated that nearly all beetles were either dead or nearly dead at a dosage of between 0.12 and 0.24 g/litre.

With the exception of carbaryl applied topically, there were no significant differences in the LD_{50}, LD_{95}, LC_{50}, or LC_{95} values of the insecticides between *C. resinosae* and *C. coniperda*. Some of the variance in toxicity values between *C. coniperda* and *C. resinosae* could be attributed to the lower mean body weights of the *C. coniperda* (mean weight of five *C. coniperda* = 0.012±0.001 g and five *C. resinosae* = 0.015±0.001 g).

On the basis of these results, it appears that azinphos-methyl, lindane, fenitrothion and possibly permethrin are potential candidates for further field testing. Of these, we would suggest that field studies be conducted with azinphos-methyl because it is already registered in Canada for a number of cone and seed insects at a dosage of 1.8 to 5.0 g a.i./l; this dosage well exceeds the dosage required in the lab to obtain a LC_{95} for both these insects. This insecticide also been widely used in southern pine seed orchards for at least 20 years (DeBarr 1994).

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TABLE I. Toxicity of topically applied insecticides to *Conophthorus resinosae* and *C. coniperda*.

Insecticide	Insects treated	Probit line slope ± SE	Toxicity (7 days after application)		Relative potency[a]
			LD_{50} (95% CL)	LD_{95} (95% CL)	
			μg/insect		
			C. resinosae		
Azinphos-methyl	270	2.38±0.34	0.005 (0.003-0.006)	0.023 (0.015-0.058)	1.00
Permethrin	270	3.67±1.00	0.025 ([b])	0.071 ([b])	0.20
Fenitrothion	270	2.76±0.54	0.040 (0.023-0.058)	0.158 (0.088-3.69)	0.12
Dimethoate	270	2.21±0.32	0.056 (0.023-0.097)	0.309 (0.156-2.65)	0.08*
Lindane	270	2.28±0.30	0.076 (0.032-0.117)	0.403 (0.251-1.24)	0.06*
Carbaryl	270	1.15±0.20	0.092 (0.064-0.137)	2.49 (0.969-16.87)	0.05
			C. coniperda		
Azinphos-methyl	270	3.31±0.46	0.002 (0.002-0.003)	0.007 (0.006-0.012)	1.00
Permethrin	270	2.60±0.32	0.017 (0.013-0.022)	0.074 (0.052-0.143)	0.12*
Fenitrothion	270	2.92±0.37	0.022 (0.014-0.028)	0.079 (0.053-0.185)	0.10*†
Dimethoate	270	2.30±0.27	0.024 (0.016-0.034)	0.125 (0.076-0.337)	0.09†
Carbaryl	270	1.22±0.20	0.026 (0.010-0.041)	0.565 (0.243-5.27)	0.05
Lindane	270	2.16±0.30	0.058 (0.018-0.093)	0.335 (0.205-1.14)	0.03

[a] Relative potency: comparison of probit line for azinphos-methyl with probit line for each insecticide by parallel line analysis. Probit lines for the insecticides followed by the same symbol are not significantly different.

[b] Confidence limits could not be computed because the value of the confidence coefficient exceeded 0.5 at the $\alpha = 0.90$ level.

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TABLE II. Toxicity of treated red pine and white pine shoots to *Conophthorus resinosae* and *C. coniperda*.

Insecticide	Insects treated	Probit line slope ± SE	Toxicity (7 days after application) LD_{50} (95% CL)	Toxicity (7 days after application) LD_{95} (95% CL)	Relative potency[a]
			g/litre		
			C. resinosae		
Azinphos-methyl	270	2.48±0.26	0.06 (0.05-0.07)	0.27 (0.20-0.41)	1.00*
Lindane	270	5.05±0.67	0.05 (0.04-0.05)	0.10 (0.08-0.13)	1.36
Fenitrothion	270	3.35±0.39	0.05 (0.04-0.06)	0.16 (0.12-0.29)	1.15*
Dimethoate	270	2.44±0.24	0.18 (0.09-0.45)	0.84 (0.36-14.70)	0.33
Carbaryl	270	2.80±0.32	0.30 (0.22-0.39)	1.17 (0.81-2.21)	0.19
Permethrin	270	1.67±0.38	0.45 (0.29-1.21)	4.27 (1.44-122.9)	0.16
			C. coniperda		
Azinphos-methyl	270	1.81±0.20	0.03 (0.02-0.04)	0.26 (0.16-0.64)	1.00
Lindane	270	3.32±0.57	0.03 (0.02-0.04)	0.09 (0.06-0.3)	1.21
Fenitrothion	270	1.76±0.23	0.06 (0.04-0.10)[b]	0.51 (0.22-6.33)[b]	0.55
Carbaryl	270	2.14±0.23	0.12 (0.06-0.19)	0.68 (0.36-3.55)	0.29*
Dimethoate	270	2.88±0.31	0.13 (0.09-0.17)	0.48 (0.32-1.03)	0.27*
Permethrin	270	1.69±0.20	0.44 (0.29-0.62)	4.17 (2.38-11.73)	0.07

[a] Relative potency: comparison of probit line for azinphos-methyl with probit line for each insecticide by parallel line analysis. Probit lines for the insecticides followed by the same symbol are not significantly different.

[b] 90% CL as the 95% CL could not be calculated.

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EVALUATION OF NEEM SEED EXTRACT AGAINST SPRUCE BUDWORM, *CHORISTONEURA FUMIFERANA* (CLEM.), IN WHITE SPRUCE, *PICEA GLAUCA* (MOENCH) VOSS., SEED ORCHARDS

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Forest Insect and Disease Surveys (1993) conducted in Ontario seed orchards during 1990 - 1993 found that the spruce budworm, *Choristoneura fumiferana* (Clem.), was the most prevalent insect pest in white spruce, *Picea glauca* (Moench) Voss., seed orchards. Defoliation by *C. fumiferana* can inhibit cone production by reducing the area available for reproductive buds to form and can reduce tree vigour and cause mortality (Morris 1963).

The botanical insecticide neem is derived from extracts of the neem or margosa tree, *Azadirachta indica* A. Juss (Meliaceae) and is a broad spectrum pesticide for phytophagous insects (Schmutterer 1990). In laboratory studies, Thomas *et al.* (1992) demonstrated that neem extracts have potential for control of spruce budworm damage. This field trial was conducted to test the effect of neem seed extract on defoliation by spruce budworm in white spruce seed orchards in comparison to dimethoate, a registered product for control of spruce cone and seed insects.

Neem seed extract, formulated as an emulsifiable concentrate and containing 2% azadirachtin, was obtained from Phero Tech Inc. (Delta, British Columbia, Canada) and Cygon® 480 (480 g a.i./L) from Cyanimid Canada Inc. (Markham, Ontario, Canada). Each of the following treatments was applied to single grafted white spruce trees in the Aubrey seed orchard[1] in a randomized block design (N=10): 1) water control, 2) 75 ppm azadirachtin, 3) 1.0 % dimethoate, and 4) untreated control. Treatments were applied to the point of runoff; azadirachtin and water on 6 June, and dimethoate on 7 June 1994. An orchard ladder and Swiss-Mex Evenspray backpack sprayer (nozzle 8004) were used to apply treatments between 6:00 and 8:00 AM. Weather conditions were clear and calm on both dates.

Larval populations and defoliation were assessed on two branches per tree; branches were randomly selected by cardinal aspect, one from the middle and one from the upper crown region. Two branch tips were clipped from each untreated control tree on 7 June and all lepidopteran larvae were collected and identified. *C. fumiferana* composed 96.7% of the total larval population. The instar[2] distribution of 100 larvae randomly sampled from untreated trees was determined as L_2- 2%, L_3- 2%, L_4- 12%, L_5- 34%, L_6- 50%.

On 12 June 1994 two branches from each tree were struck two times and the number of larvae collected on a 45 x 70 cm piece of corrugated cardboard were counted. The majority of larvae were 5th and 6th instars that readily "spun down" upon agitation. In comparison to control trees, neem treatment did not reduce the number of larvae collected (25.5±1.8 and 22.7±3.2, respectively, $\bar{x}$ ± S.E.) (P=0.46, t-test, N=10) whereas the dimethoate treatment essentially eliminated larval populations (0.3±0.2) .

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[1] Ontario Ministry of Natural Resources, Dryden, Ontario, established from 1975-1984, now averaging 4-6 m in height.

[2] Head capsule measurements (Bean and Batzer 1957) were used to identify larval instars.

TABLE I. Mean number of *Choristoneura fumiferana* larvae and pupae collected from two 40 cm branch tips sampled per tree (N=10 trees), 22 days after treatment.

Treatment	Number of *C. fumiferana* per two branches*	
	Larvae ($\bar{x}$ ± S.E.)	Pupae† ($\bar{x}$ ± S.E.)
Control	0.4 ± 0.2a	27.1 ± 2.8a
Azadirachtin 75 ppm	6.4 ± 0.8b	1.5 ± 0.2b
Dimethoate 1.0%	0.0 ± 0.0a	0.3 ± 0.1b

* Means within a column followed by the same letter are not significantly different, $\alpha = 0.05$, Friedman test.

† Combined number of living pupae and empty pupal cases.

On 28 June (22 days post-treatment) two 40 cm branch tips were cut from each tree and the number of larvae, pupae and empty pupal cases were recorded. The combination of fewer pupae and greater numbers of larvae on the neem treated trees versus the control trees indicated delayed larval development (Table I). Defoliation of the cut branch tips was assessed by removing the new vegetative shoots and rating each into one of four defoliation classes: 1) none, 2) light (1-33%), 3) moderate (34-67%), and 4) severe (68-100%). Treatment with neem (75 ppm azadirachtin) and 1.0% dimethoate reduced defoliation by *C. fumiferana*; both the proportion of shoots fed upon and the amount of feeding on individual shoots were significantly lower in comparison to control trees (Table II).

TABLE II. Defoliation of white spruce trees by *Choristoneura fumiferana* in the Aubrey seed orchard, Dryden, Ontario. Defoliation was assessed by the percentage of new shoots (pooled from two 40 cm branch tips) with feeding damage and by the distribution of damaged shoots into defoliation classes (light, 1-33%; moderate, 34-67%; and severe, 68-100%). Treatments were applied on 6-7 June, 1994, and defoliation was assessed on 28 June, 1994.

Treatment	% New shoots defoliated ($\bar{x}$ ± S.E.)*	% of new shoots within defoliation classes ($\bar{x}$ ± S.E.)		
		Light	Moderate	Severe
Control	90.7 ± 8.6a	12.3 ± 3.0a	26.5 ± 3.8a	61.2 ± 6.0a
Azadirachtin 75 ppm	61.8 ± 6.8b	35.7 ± 3.3b	26.9 ± 3.3a	37.2 ± 4.7b
Dimethoate 1.0%	68.2 ± 19.8b	27.3 ± 3.3b	32.5 ± 3.3a	40.1 ± 2.9b

* Means within a column followed by the same letter are not significantly different, $\alpha = 0.05$, Bonferroni t-test.

In contrast to treatment with neem, dimethoate resulted in rapid larval mortality in the laboratory (100% mortality within 24 hours on treated foliage). Neem treatment, without causing rapid larval mortality, still protected foliage as well as did dimethoate. Azadirachtin in artificial diet reduced consumption by *C. fumiferana* 6th instar larvae in a dose dependent manner with a concentration of 19 ppm required to reduce feeding by 50% (Thomas *et al.* 1992). Other laboratory studies with *C. fumiferana* indicate that the ingestion of small quantities of neem extract may induce a physiological effect which inhibits further feeding (Blair Helson, pers. comm.).

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SOME PHYTOPHAGOUS INSECTS FOUND ON *RUDBECKIA HIRTA* AND *CHRYSANTHEMUM LEUCANTHEMUM* IN THE OTTAWA/HULL AREA

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The ox-eye daisy, *Chrysanthemum leucanthemum* (Asteraceae), and the black-eyed Susan, *Rudbeckia hirta* (Asteraceae), are mainly found in open fields, roadsides and on waste lands (Gleason 1968). Both species have been used to treat wounds, fever, urinary tract infections and dermatomucosal diseases (Hussey 1974; Caceres *et al.* 1987a; Caceres *et al.* 1987b) while *R. hirta* has been used as an abortifacient agent by Spanish New Mexicans (Conway and Slocumb 1979). Insecticidal and insect repellent properties have also been reported for both plants (Metzger and Grant 1932; Nawrot 1983; Guillet *et al.* 1995).

In this paper, we report on the phytophagous insects that colonize *C. leucanthemum* and *R. hirta* in the geographical area of Ottawa/Hull. As these insects are adapted to life on phototoxic plants, they constitute relevant models for further investigations on the behavioral and/or biochemical adaptations that allow them to tolerate these highly noxious phototoxins (see review in Aucoin *et al.* 1995).

Phytophagous insect on *Chrysanthemum leucanthemum* inflorescences

The red-banded leaf roller, *Argyrotaenia velutinana* Walk. (Lepidoptera: Tortricidae), has been observed on the inflorescences of *C. leucanthemum* on each of the 10 sites investigated in the 1992 and 1993 seasons. While *A. velutinana* is described as a polyphagous insect of deciduous trees and more specifically of apple trees (Chapman and Lienk 1971), the observations made in abandoned fields showed that this species has a high specificity for the ox-eye daisy: more than 97% of the larvae observed on herbaceous plants (n=652) were on *C. leucanthemum*. Between 1% and 3% of the total inflorescences of *C. leucanthemum* were colonized by at least one larva of *A. velutinana* in open sites while this proportion increased up to 20% in shaded areas (Guillet *et al.* 1995). The ox-eye daisy is a major host plant in abandoned fields only for the first larval generation of *A. velutinana* as *C. leucanthemum* is not available later in the season when the second generation occurs.

Phytophagous insect on *Chrysanthemum leucanthemum* and *Rudbeckia hirta* inflorescences

Larvae of *Sparganothis sulfureana* (Clem.) (Lepidoptera: Tortricidae) were initially observed on *C. leucanthemum* heads. Later in the summer, some of the last instars were observed to transfer selectively to the inflorescences of *R. hirta*. This host plant switching occurred in 21% (n=98) and 42% (n=149) of the last instar larvae in 1992 and 1993 seasons respectively. In behavior resembling *A. velutinana*, larvae rolled the petals of the inflorescences to build an opaque shelter in which they developed to the last instar. Larvae were observed during the last two weeks of July and the first two weeks of August in 1992 and 1993. In 1992, more than 98% of the

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larvae (n=247) were observed on either *R. hirta* or *C. leucanthemum* on which they fed mainly on the seeds. To our knowledge, this is the first time that *C. leucanthemum* and *R. hirta* are reported as the primary hosts of *S. sulfureana*. One hundred and twenty eight 4th and 5th instars were collected in field and fed fresh *C. leucanthemum* plants in an incubator (photoperiod of 16 hours, 25°C at day and 20°C at night, 70-75% RH), from which 117 pupae were obtained and 74 adults emerged.

Phytophagous insects on *Rudbeckia hirta* inflorescences.

Chlorochlamys chloroleucaria (Gn.) (Lepidoptera: Geometridae) larval development on *R. hirta* took approximately 40 days in the field. Larvae were observed from the 29th of June to the 30th of August in 1992 in the Ottawa/Hull area. Only three larvae of the second generation were observed on *R. hirta*. Less than 3% (n=307) of the larvae were found on host plants other than *R. hirta* (*C. leucanthemum*, *Solidago canadensis*, *Achillea millefolium*, *Rubus idaeus* and *Coreopsis* sp.). Larvae were observed to stay on the top of the inflorescences on which they preferentially fed on the non-toxic pollen (Guillet *et al.* 1995). Such behavior constantly exposes the larvae to a parasitoid, *Cotesia* sp. (Hymenoptera: Braconidae), which has not been reported previously. Of the 97 4th and 5th instars grown in an incubator (conditions as above) on *R. hirta*, 88 pupae and 44 adults were obtained while 29 adults of *Cotesia* sp. emerged from 29 larvae. Mean times of pupal incubation and of adult lifetime (n=44) were 20.4 and 10.4 days respectively. From 44 adults, 22 eggs were individually laid on the ligulate corollas of *R. hirta* placed in the incubator.

During the second half of July, another species, *Eupithecia miserulata* Grote (Lepidoptera: Geometridae), was also observed to feed on the pollen of *R. hirta*. This generalist insect has already been described as feeding on *R. hirta* and other herbaceous plants as well as trees (Forbes 1948; Tietz 1972).

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BOOK REVIEW

Biological Control with Egg Parasitoids 1994 *Edited by* E. Wajnberg and S.A. Hassan. CAB International, Wallingford, UK. xiv + 286 pp. $103.20 CAN

Egg parasitoids, especially in the genus *Trichogramma*, have been employed extensively in biological control programs worldwide. Although there have been several international meetings with resulting publication of proceedings, an authoritative review of the field has been long overdue. *Biological Control with Egg Parasitoids* edited by E. Wajnberg and S.A. Hassan addresses this need.

Biological Control with Egg Parasitoids is intended "to provide a broad overview of the use and potential of egg parasitoids in biological control". The editors have done a very good job at realizing this objective. The twelve chapters, written by members of an International Organization for Biological Control working group, are comprehensive and cover most of the pertinent scientific issues in the practice of biological control with egg parasitoids.

The book opens with an excellent review of the systematics of *Trichogramma* and related genera by J. Pinto and R. Stouthamer. The authors focus on synoptic characteristics of the group and identify many of the practical difficulties with identification. The authors critique the biological control community for its parochial view of *Trichogramma* and end with a plea for a more global perspective on the group if we hope to achieve taxonomic stability. Chapter 2 is a survey of the worldwide use of *Trichogramma* (L-Y Li) which gives a general sense of the range of target hosts and areas treated. Included in the chapter is a compilation of release rates, pest reductions, and efficacy estimates for inundative release programs conducted in China since 1982.

The next four chapters deal with more technical aspects of particular concern to modern commercialization of biological control with egg parasitoids. Hassan discusses strategies to select *Trichogramma* species for use in biological control (Chapter 3). Although it is at first uncertain as to whether Hassan is discussing species or strain selection, his description of simple laboratory assay methods which correlate well to expected field efficacy could be used in either case. A useful review of rearing egg parasitoids on artificial diet by S. Grenier includes a discussion of oviposition stimulants and some of the limitations that beset this approach to parasitoid production (Chapter 4). Quality control in parasitoid production is treated ably by F. Bigler (Chapter 5). The author emphasizes the importance of regular laboratory testing of several simple characteristics to identify deterioration of stock. He gives a case study to clarify the process. The valuable contribution of this chapter is Bigler's contention that mass production of egg parasitoids is an industrial process but with a variable and dynamic biological product. This group of chapters is appropriately completed by a comprehensive review of release methods for egg parasitoids by S. Smith (Chapter 6). Her chapter is one of the few that goes beyond a review of published material to provide explicit ideas on future needs.

Chapter 7 by F. Bin is a brief review of biological control with egg parasitoids other than *Trichogramma*. This chapter is disappointing as it does not do justice to the many classical introductions employing egg parasitoids but relies on a brief review of another review on the subject. In this respect, the chapter reflects this working group's focus on only a few species of one genus of parasitoids employed mostly in inundative tactics.

The next two chapters range from a cursory and somewhat unsatisfactory treatment of habitat location by *Trichogramma* (D. Nordlund, Chapter 8) to a detailed investigation of host recognition and acceptance (J. Schmidt, Chapter 9). The latter is an excellent review but unfortunately does

not bring the impressively detailed knowledge of *Trichogramma* behaviour into the practical context of biological control. The distinctiveness of the physiological interactions between egg parasitoids and their hosts is given adequately by S.B. Vinson (Chapter 10) and overwintering strategies are discussed by G. Boivin (Chapter 11). In contrast to the comments made about the chapter by Schmidt, there is a dearth of specific information on physiology and overwintering of egg parasitoids despite the importance of these subjects to production and deployment of egg parasitoids in inundative releases. Despite this, both authors are able to relate what is known to biological control and to raise valuable questions for future research.

The final chapter by E. Wajnberg describes a quantitative approach to identifying genetic variability within populations of *Trichogramma* (Chapter 12). The approach is pragmatic and not particularly explanatory but Wajnberg does focus his interest on traits of fundamental ecological importance to the process of parasitism and this is welcomed.

Biological Control with Egg Parasitoids avoids many of the shortcomings commonly associated with multi-author books. There is little redundancy and collectively the chapters cover much of the area of current interest in egg parasitoids arranged in a logical sequence. Nonetheless there are some subject areas where one feels more attention is deserved. Pest management by any method is an attempt to alter population dynamics. With biological control, pest management is an attempt to use the population dynamics of one organism to alter another's. With the exception of a brief section by S. Smith (Chapter 6), this reality is inadequately emphasized in this book. Nor was the opportunity taken to review patterns of parasitism in natural, undisturbed populations in order to identify pest life systems in which egg parasitism is or is not important. On the applied side, a more critical evaluation of the effectiveness of biological control with egg parasitoids would have been a welcome addition to this book.

Regrettably, but perhaps not surprisingly, is the omission of two of the most-discussed issues of biological control with egg parasitoids at the meetings I have attended in the past few years: the economics of industrial production and marketing of egg parasitoids, and the environmental impact of biological control as it relates to impending regulatory restrictions.

Despite these criticisms, *Biological Control with Egg Parasitoids* is the best review of the subject we are likely to have for some time. It should interest both researchers and practitioners. It should also serve hopefully as a starting point for new and critical research directions in this challenging approach to rational pest management.

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Fly Fishing the Grand River 1995 by Ian D. Martin and Jane E. Rutherford. The Usual Press. 56 pp.

I have lived a dozen years on the banks of the Grand River, and spent countless evenings bug-watching in the backyard riffle that was mine alone until a few years ago, when a massive stocking of brown trout turned my stretch of river into a fly fisher's mecca. The resultant daily flow of trespassers disturbed me at first, but I soon learned that many of my uninvited guests had a good conversational knowledge of aquatic insects, and some really surprised me with their interest in

entomology. Martin and Rutherford's book, *Fly Fishing the Grand River*, seems aimed directly at those pleasant anglers who wade through my riffle with excited comments about Hendricksons, Speckled Sedges, and the Little Black Caddis. Martin and Rutherford have pulled together the "results of several years of sample collection and identification" and "tried to cover all the major hatches and fish foods of the Grand River trout waters". It is not every day I see a primarily entomological book dealing specifically with my backyard, so I was quite enthusiastic about receiving this book.

The first thing I noticed about the book was its format. Described as a vest pocket guide, it is appropriately spiral bound under robust-looking covers with each page divided into an 8 cm text column, and a 4.5 cm column along the right margin bearing the heading "highlights". The highlights columns are most empty space, but many include useful-looking black silhouettes of the insects under discussion. Closer inspection shows that these silhouette drawings are worse than a waste of space, as the same drawings are repeated over and over with different captions, some of which could not possibly match the species depicted. Every drawing of a mayfly dun has 3 caudal filaments; every drawing of a mayfly spinner has 2 caudal filaments and 4 wings. Every drawing of an adult caddisfly is the same, whether labelled as a leptocerid, hydropsychid or limnephilid. Some of the highlight drawings, such as the immatures on page 6, are useful.

The text part of the book begins with a short glossary, a short history of the Grand, and a few comments on the very useful map conveniently printed on the back cover. It then proceeds into discussions of the main mayfly species, organized chronologically. Similar coverage of the main caddisfly species follows. A few pages are given over to other taxa, two pages are given to extremely interesting tables giving timing of mayfly and caddisfly hatches, then the last eight pages are given to a rather heterogeneous series of colour plates.

The species by species accounts are informal but well written, and reflect the authors' personal experience with the insects concerned. Basic biology is neatly combined with fishing lore, with both entomologist's and fly fisher's terms used. I enjoyed the discussions, but I suspect the average angler will be frustrated with the lack of criteria for separating one taxa from another, and the odd bit of entomological jargon may jangle fishermen despite the glossary ("heptageniid", for example, would sound strange to someone unfamiliar with the concept of a family Heptageniidae). All in all, the text is a good read, full of the insights that result from the authors' hybrid interests in entomology and fishing.

The heart of the book is the hatch tables on pages 54 and 55 - interesting, well presented and of great practical value in identifying the hatch on any given date. The colour plates which follow are of mixed value. Some of the photos are of poor quality, but it is still useful to have colour photos of some of the species discussed side by side with pictures of the flies tied to mimic them. The captions could have been more informative, perhaps pointing out what characterizes the species illustrated. These are small deficiencies, which I hope the authors will correct in a second edition. This kind of informative yet accessible book can only increase public appreciation for the science of entomology. I would recommend this little book for anyone interested in fishing or bug-watching on the Grand or similar southern Ontario rivers.

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THE ENTOMOLOGICAL SOCIETY OF ONTARIO
CONSTITUTION AND BY-LAWS
(as amended and approved 23 September 1995)

The Entomological Society of Ontario was incorporated on the 15th of February, 1871, by section 9 of Chapter 23 of Statutes of Ontario, 1871, (34 Vic., Cap. 23) being an Act to amend the Agricultural and Arts Act as follows:

9. That the following section from the Act described the purpose of the Society:

"The Society now existing known as the 'Entomological Society of Canada', may organize and form themselves into a society, comprising not less than twenty five members, and paying an annual subscription of not less than one dollar each, to be known as 'The Entomological Society of Ontario', and shall have power to adopt a constitution, and make By-Laws for the admission of members, and for its guidance and proper management and the promotion of any objects consistent with the study of Entomology, and its practice bearing upon the agricultural and horticultural interests of the Province of Ontario and not inconsistent with the laws of the province; and on filing a copy of such constitution and By-Laws with the Commissioner of Agriculture such society shall become a body corporate under this Act."

CONSTITUTION

Name — ARTICLE 1 (1) The corporation shall be known as the Entomological Society of Ontario, hereinafter called the Society.

(2) The headquarters and library of the Society shall be situated at the Ontario Agricultural College of the University of Guelph.

(3) The seal of the Society bears two concentric circles, the inner enclosing a line drawing of a monarch butterfly superimposed on an outline map of Ontario; the outer ring contains the inscription in Old English Type

Entomological Society of Ontario 1863

Objects — ARTICLE 2 The objects of the Society shall be to serve as an association of persons interested in the study of insects and to promote the science of entomology in all its aspects, with special emphasis upon the interests of the Province of Ontario.

Membership — ARTICLE 3 (1) Membership is open to any person interested in entomology upon payment of the prescribed dues.

ARTICLE 3 (2) The classes and conditions of membership and appropriate dues for each class shall be established by By-Law.

Fellows

ARTICLE 4 A Member or former Member who has made an outstanding contribution to the advancement of entomology shall be eligible for election as a Fellow of the Society, the mode of election being determined by By-Law.

Governing Board

ARTICLE 5 The general management of the Society shall be vested in a Governing Board consisting of the Directors and Officers: President, Past-President, President-Elect, Secretary and Treasurer or Secretary-Treasurer and ex-officio members appointed according to By-Law. The number of Directors, their mode of election, and the mode of election of the officers shall be determined by By-Law.

Meetings

ARTICLE 6 (1) The Society shall hold an Annual Meeting at such time and place as may be determined by By-Law.

(2) At each Annual Meeting, the Governing Board shall present a full report of their proceedings, and of the Society Proceedings, and a detailed statement of the receipts and expenditures for the previous year, and of the assets and liabilities, duly audited.

(3) Other meetings may be called under the conditions established by By-Law.

Security by the Treasurer

ARTICLE 7 (1) The Treasurer of the Society, before entering upon the the duties of the office, shall give such security, either by joint covenant with one or more sureties, or otherwise, as the Governing Board may deem necessary, for the faithful performance of duties and especially for the due accounting for and paying over of all monies which may come into hands.

(2) It shall be the duty of the Governing Board in each and every year to enquire into the sufficiency of the security given by the Treasurer and to report thereon and where the same Treasurer for the Society is reappointed from year to year, the reappointment shall continue valid as against the parties thereto.

(3) If the Governing Board of the Society neglects to procure and maintain proper and sufficient security its members shall be personally responsible for all the funds of the Society in the possession of the Treasurer.

Election of Auditors

ARTICLE 8 (1) The Society, at the Annual Meeting, shall elect an auditor or auditors to audit the accounts of the Society, to hold office until the next Annual Meeting.

(2) Auditors shall be eligible for re-election.

(3) The fiscal period of the Society shall be the calendar year.

Amendment of Constitution

ARTICLE 9 (1) Proposals to amend or repeal the Constitution of the Society shall be made by the Governing Board or by ten Members in good standing in a signed letter to the Secretary, and shall be transmitted to the Members with the notice of the next following Annual Meeting.

(2) The Constitution may be amended or repealed by a two-thirds majority vote of Members, the vote being taken subsequent to a discussion at an Annual Meeting, by a letter ballot distributed not later than the ballot for the next annual election; and providing further that such repeal or amendment shall not be in force or acted upon until approved by the Minister of Agriculture and Food of Ontario.

Amendment of the By-Laws

ARTICLE 10 (1) Proposals to amend the By-Laws may originate from or be or be presented to the Governing Board, and shall be transmitted to the Members with the notice of the next following Annual Meeting.

(2) By-Laws may be amended by a majority vote of Members at the Annual Meeting, or by a mail ballot as decided by the Governing Board.

(3) Approved amendments to the By-Laws come into effect upon approval by the Minister of Agriculture and Food of Ontario.

BY-LAWS

Membership

By-Law 1 (1) The Society shall have the following classes of membership consisting of those persons with a professional or amateur interest in entomology.

(a) **regular membership**, consisting of those who have paid the prescribed dues and are entitled to all the privileges of the Society, including a single vote in any general ballot of the membership, election to an office of the Society, and a copy of the Society Proceedings.

By-Law 1

(b) **honourary membership**, consisting of Members of the Society who, upon retirement, wish to continue with all rights and privileges of the Society, other than voting; there are no dues.

(c) **sustaining membership**, consisting of those corporations, companies and like bodies that are interested in promoting the objectives of the Society and have paid the prescribed dues. Rights and privileges are those of a single regular Member.

(d) **fellows**, consisting of those persons accepted as Fellows of the Society through elective procedures outlined elsewhere in these By-Laws. Rights and privileges are as for Regular Members; there are no dues.

(e) **student membership**, consisting of Members who are currently registered as students at an academic institution and are entitled to a single vote but will not receive the Society Proceedings.

(2) Acceptance into membership in any class shall be subject to the approval of the Governing Board.

(3) (a) Dues for the different classes of membership shall be determined from time to time by resolution of the Governing Board and fixed and approved by By-Law passed at an annual meeting.

(b) Membership dues shall be payable to the Treasurer January 1st for the current year.

(4) A Member may resign from the Society by delivering a written resignation to the Secretary, but upon resigning shall not receive any refund of dues.

(5) A Member who has not paid the membership dues in full by the last day of the fiscal year notice mailed to the last known mailing address cease to be a member, but may be re-instated upon payment of unpaid dues in full, and a person who ceased to be a member of the Society for failure to pay dues in full and re-applies for membership, shall submit payment of all dues payable during the year prior to the re-application for membership as well as dues for the current year.

Annual and Special General Meetings — By-Law 2

(1) The time and place of the Annual Meeting shall be determined by a By-Law passed at an Annual Meeting. Such an Annual Meeting shall normally be held in September, October, November or December.

(2) A special meeting of the Society may be called by the Governing Board or at the written request of fifteen Members of the Society, and shall be held at the headquarters of the Society.

(3) Notice in writing of the time and place of the Annual Meeting or a special meeting shall be mailed by the Secretary to the Members not less than fourteen days in advance of the holding of such meetings.

(4) The Secretary shall include in any notice respecting a special meeting a statement of the business to be transacted and no other business shall be transacted at such a meeting.

(5) A Member may vote by proxy at a special meeting provided that the proxy, who is a Society member in good standing is named in a signed statement delivered to the Secretary in advance of the meeting.

(6) An Annual or special Meeting, on a majority vote, may be closed to all persons not Members of the Society.

(7) 15 Members of the Society shall form a quorum at an Annual Meeting or at a special meeting.

Officers — By-Law 3

(1) The Officers of the Society shall be the President, Past-President, President-Elect, Secretary and Treasurer or Secretary-Treasurer.

(2) (a) The President, President-Elect and Past-President shall hold office for one year.

(b) The President shall be that person who has most recently completed a term of office as President-Elect. A vacancy shall be filled by the President-Elect who will then serve the normal term as President.

By-Law 3 (2) (c) The President-Elect shall be that person who was most recently elected to this office. After one term the President-Elect shall become the President. A vacancy shall be offered to the person with the next highest number of votes in the most recent election.

(d) The Past-President shall be that person who has most recently completed a term of office as President. A vacancy shall be filled by the person who has most recently completed a term of office as Past-President.

(e) The Governing Board shall, from among themselves or otherwise, elect a Secretary and a Treasurer or a Secretary-Treasurer.

Governing Board

By-Law 4 (1) The Governing Board shall be comprised of six Directors and the Officers of the Society.

(2) The normal term of office of a Director shall be three years.

(3) The Governing Board shall have full power to act for and on behalf of the Society, and all grants of money and other funds of the Society shall be received and expended under its direction subject to the By-Laws of the Society.

(4) The Board may delegate any of its powers to an Executive Committee composed by the President, President-Elect, Past-President and the Secretary and Treasurer or Secretary-Treasurer but any action taken on powers so delegated shall be recorded in minutes and shall be presented for approval by motion at a meeting of the Governing Board before the next Annual Meeting.

(5) Meetings of the Governing Board of the Society may be called by the President thereof, or in the absence or on the neglect, by the President-Elect, or by the Past-President or Secretary in order of authority. In the absence or on the neglect of the President and President Elect, or in the absence or on the neglect of the Officers of the Society, by any three Directors of the Society of which meeting at least seven days notice shall be given to each Officer and Director.

(6) A majority of the Officers and Directors shall form a quorum.

By-Law 4 (7) The Directors elected at an Annual Meeting shall take office at the close of that Meeting, and at their first meeting shall install the previous President-Elect as President, and the recently elected President-Elect.

Election of President-Elect and Directors

By-Law 5 (1) The Members of the Society, from persons eligible for regular membership, shall elect every year a President-Elect and two Directors by mail ballot, as follows:

(a) The governing Board shall appoint a Nominating Committee comprised of a Chair and no fewer than two other Members of the Society.

(b) The Nominating Committee shall nominate no fewer than two Members as President-Elect, and no fewer than three Members as Directors, and shall deliver these nominations, together with written acceptances by the nominees and a short biographical sketch of each nominee to the Secretary not later than the first day of February.

(c) A list of nominations made by the Nominating Committee and the accompanying biographical material shall be mailed to the Members by the Secretary not later than the tenth day of April.

(d) Members of the Society may nominate additional persons for Directors and for President-Elect provided that each nomination is made by no fewer than five Members and is accompanied by a written acceptance of the nomination by the nominee and a short biographical sketch of each nominee and is delivered to the Secretary not later than the first day of May.

(e) The Secretary shall prepare and mail to Members of the Society whose dues for the current year have been paid, not later than the fifteenth day of June, a ballot for the election of the President-Elect and the Directors that contains the names of the nominees for each office arranged in alphabetical order, and shall provide sufficient instructions and envelopes to ensure the secrecy of the vote.

(f) The ballots shall be returned to the Secretary not later than the fifteenth day of July.

By-Law 5 (1) (g) The Governing Board shall appoint no fewer than two Members of the Society to act as scrutineers and to be present when the Secretary opens and counts the ballots.

(h) Each question on the ballot constitutes a separate ballot and spoiling a vote for one question does not spoil the other questions. Each question on the ballot shall be determined by a simple majority of the votes cast unless otherwise specified in the Constitution and By-Laws.

(i) In case of a tied vote for the elections of the President and Directors, the Past-President who chairs the nominating committee and does not vote during the election will cast the deciding vote.

(j) The Secretary shall notify all candidates of the results of the election.

(k) The names of the elected candidates shall be presented at the next Annual Meeting. The election of the President-Elect, and two Directors, and the appointment of the four previously-elected Directors to a second term or third term shall be formally ratified by the motion at the Annual Meeting.

(2) Directors shall be eligible for re-election, but shall not hold office for more than six years consecutively.

(3) If a Director, after one year or two years in office, is elected as President-Elect, the Director's vacancy shall be offered to the runner-up.

(4) A vacancy occurring by death or resignation, or failure to qualify as a Member, of any Officer or Director may be filled by the remaining Officers and Directors of the Society, and it shall be the duty of such Officers and Directors to nominate and appoint a fit and proper person to fill the office for the unexpired term of the person so dying or resigning; but, in the event of the remaining Officers and Directors being insufficient to form a quorum, or, if, for any reason, a quorum cannot be obtained, then persons to fill the vacant offices shall be elected in the manner provided in subsection 6.

By-Law 5

(5) In the event of an election of any Directors and Officers of the Society not being held at the time and place directed by By-Law or being for any reason illegal or void, the persons in office at the time when such Directors and Officers have been elected, shall continue to be the Governing Board of the Society until their successors are legally appointed.

(6) In the event of any such non-election or illegal election, a special meeting of the Members of the Society shall be called in the manner provided by By-Law, for the election of such Directors and Officers, and at such meeting the election of Directors and Officers shall take place, and the persons elected shall thenceforth, until their successors are appointed, be the Directors and Officers of the Society.

(7) The Society may elect as Director or President-Elect a person not a Member of the Society, but the person so elected must, within ten days, become a Member, and henceforth shall be entitled to act as a Director or President-Elect respectively.

(8) The Society may by By-Law provide that only those Members who have paid their dues at least one week in advance of the Meeting shall be qualified to vote at the Annual Meeting for the election of Directors and President-Elect.

(9) The above procedure for election of Directors and President-Elect shall ensure that one President-Elect shall be elected from at least two candidates and two Directors shall be elected from at least three candidates on the ballot. The President-Elect will serve for one year prior to taking office as President and each Director shall serve for a three-year term.

Representative to the Entomological Society of Canada

By-Law 6

The Governing Board shall appoint at the appropriate times a Member of the Society to act as a Director of the Entomological Society of Canada who shall normally serve a three-year term. This person shall be ex-officio a Member of the Governing Board of the Society.

Committees and Ex-officio Appointments

By-Law 7

(1) The Governing Board shall appoint:

(a) A Librarian who shall be responsible for the orderly maintenance of the library and archives.

By-Law 7 (1) (b) A Publications Committee comprised of a Chair and no fewer than two other Members of the Society that shall be responsible for all publications of the Society including the Society Proceedings and shall act as an editorial board; and the Chair shall be the editor of the Proceedings.

(c) Such other ad-hoc committees as it deems necessary; chairs of ad-hoc committees shall be members ex-officio of the Governing Board.

(2) Chair of such committees appointed by the Governing Board shall be Members ex officio of the Governing Board.

Election By-Law 8 (1) Fellows are Members or former Members who have made an outstanding contribution to the advancement of entomology.

(a) Fellows shall be elected if at least two-thirds of the votes cast in a secret mail ballot are in the affirmative.

(b) A person may be nominated as a Fellow by no fewer than three members of the Society.

(c) The maximum number of Fellows of the Society shall be limited to ten at any one time and no more than two shall be elected in any one year.

(d) Names of nominees received by the Secretary and approved by two-thirds of the votes at a meeting of the Governing Board shall be placed on a ballot prepared by the Secretary and mailed to the Members with the next ballot for the election of Directors.

(e) The ballots shall be returned to the Secretary not later than the fifteenth day of July and shall be opened and counted at the same time and under the same scrutiny as the ballots for the election of Directors.

(f) The Secretary shall announce at the Annual Meeting the names of the persons elected as Fellows. Certificates of Fellowship in the Society shall be presented.

(g) The names of Fellows of the Society shall be published annually in the Society Proceedings.

Duties of Officers By-Law 9

(1) The President shall preside at all meetings of the Society and of the Governing Board and of the Executive Committee.

(2) The President-Elect shall carry out the duties of the President in the latter's absence for any cause.

(3) The Secretary shall

(a) record the minutes of the Annual Meeting and all meetings of the Governing Board and the Executive Committee;

(b) maintain the list of Members of the Society; and

(c) perform such other duties as the Governing Board shall determine.

(4) The Treasurer shall

(a) have charge of the funds and other assets of the Society;

(b) make all disbursements for the Society;

(c) receive dues and other monies payable to the Society;

(d) keep accurate records of receipts and expenditures; and

(e) prepare and present to the Annual Meeting a statement of receipts and expenditures, and of the assets and liabilities, duly audited.

President's Prize By-Law 10

(1) A sum of money, the amount to be approved by the Board of Governors each year, will be given to a graduate, undergraduate student or graduand of the year who is a Society member and is deemed to present the best paper on an aspect of entomology at the Annual Meeting of the Society.

(a) Titles of papers to be considered for the President's Prize shall be submitted on appropriate forms provided by the Committee Chair responsible for the Programme of the Annual Meeting by the deadline for receipt of papers for the Annual Meeting as stated by that Programme Committee.

By-Law 10 (1) (b) The President shall, at the beginning of the Annual Meeting, select a panel of impartial judges to hear the student papers submitted for the President's Prize, and to select the paper to be named for the prize.

(c) The award shall be presented at an appropriate time before the close of the Annual Meeting.

INSTRUCTIONS TO AUTHORS

The Proceedings of the Entomological Society of Ontario is a fully refereed publication. Although the *Proceedings* are published once a year, manuscripts are welcomed at any time. The following set of instructions is intended to assist in writing and preparation of manuscripts. The style is quite standard and reference to recent volumes of the *Proceedings* will assist in case of difficulty. Special problems should be brought to the Editor's attention at the time of submission of the manuscript.

General. Articles accepted for publication are either in English or French with an English abstract. At least one author shall be a member in good standing of the Society. Manuscripts shall not be offered for prior or simultaneous publication elsewhere, and the Editor should be told if manuscripts have been refused elsewhere. Authors shall write as concisely as possible, omit material not essential to the main theme of the paper, keep footnotes to a minimum, and explain in the letter of transmittal the general subject and any presubmission reviews.

Text. Manuscripts should be typed or printed (dot-matrix printing is acceptable only if dark), double-spaced throughout (including captions, references, synonymies, and footnotes) on one side of the paper. Margins should be at least 25 mm at the top, right, left, and bottom. The use of manuscript paper with numbered lines facilitates review. The original and two review copies of the text should be submitted to the Editor. The author should retain another copy. Spelling within one article should consistently conform to usage recommended in *either* the Oxford *or* Webster's New International dictionary. Except in tables, figures, or quotations, dates should be written in the form '24 May 1985, 27 September', etc. Reference to illustrations should be in the form of 'Figure 5' within a sentence or (Fig. 5) when in parentheses. Reference to tables should be in the Form of 'Table IV'. References are noted as 'Black (1892)', '(White 1984)', '(Green 1967, 1972a,b)' or '(Brown and Grey 1956; Smith 1967)' in chronological order for multiple citations within one set of parentheses. Footnotes should be typed at the bottom of the page to which they apply, and be separated from the text by a line.

Computers. The editor strongly encourages the use of computers for manuscript preparation, preferably in Word Perfect format. Hardcopy, printed manuscripts must be submitted for review purposes. After final acceptance, the final manuscript must be submitted on a 3.5" disk containing only that manuscript plus files for accompanying graphics if applicable. The name of the file(s) on the disk plus the name and version number of the word processing and/or graphics package used must be given. Typesetting directly from disk-copy reduces errors and speeds up publication.

Abbreviations. Except for those which are generally recognized, or defined within the text for the sake of brevity (e.g. JPBW for Jack Pine Budworm), abbreviations should be avoided. **Units of measurement** should be metric and abbreviated according to the Canadian national standards.

Taxonomic papers should confirm to those in recent issues of the *Proceedings* (see Volume 124 (1993)).

Abstract. Articles exceeding two printed pages, except scientific notes, must be preceded by an informative abstract, about 3% as long as the text, but no longer than 300 words. Articles in French should have two abstracts, one in French, the other in English.

Acknowledgements should be short and grouped in a paragraph at the end of the text.

References should be listed in alphabetical order of authors at the end of the manuscript in the form used in the *Proceedings* Volume 125 (1994). Any reference not directly consulted by the author should be preceded by an asterisk. The full title for each reference must be given, and the complete pagination for all items, including books. Pages or figures should not be cited in references but, if necessary, in the text as '(Perkins 1984, p. 153, fig. 5)'. **The names of serials and periodicals should be written out in full**.

Type Styles. Words to be italicized should be underlined once, or typed in italics. Words to be set in CAPITALS should be typed in CAPITALS. Special type styles requested by the authors should be noted in the margin of the manuscript at the appropriate place.

Tables should be numbered in roman numerals and grouped at the end of the text, each on a separate page. The title of each table should follow the journal's conventions for capitals and punctuation, and should explain the contents of the table. The approximate position of each table should be indicated in the text.

Illustrations, general. Originals for line drawings and halftones, and two clear copies of each for reviewers must be submitted. Each figure or group of figures should bear the author's name, title of the article, and figure number. Illustrations and lettering should be scaled to allow reduction. The lettering, which becomes an integral part of the engraving, must be carefully distinguished from the caption, which is set in type and which must be submitted apart from the illustrations.

Line drawings should be made with india ink, transfers or laser printers on good quality white surfaces. Graphs may be submitted on squared paper only if the grid lines are light blue. If done electronically, files for the line drawings or graphs should be submitted along with the manuscript file on disk, preferably in TIF or PCX format but other formats are acceptable. Lettering, symbols, and shading should be large enough that they will not "block in" when reduced. Lettering should be neat, uniform, and meticulously prepared.

Halftones should be photographic prints of high contrast on glossy paper. Negatives or unmounted photographs are unacceptable. If more than one photograph is to appear on a page, the component prints must be numbered and mounted abutting on a card. To achieve the best appearance, lettering should be kept to a minimum.

Captions for all illustrations should be numbered consecutively (Figure 1 etc.) and typed in order, at the end of the manuscript, a separate paragraph being devoted to each page of illustrations. Captions must be attached to illustrations.

Scientific notes are welcomed. The same standards apply as for full papers except that abstracts are not included.

Review Policy and Process. All manuscripts published are reviewed by at least two reviewers. The Editor, or an Associate Editor, selects those reviewers and does not disclose their names. The editor decides to accept, reject, or return for revision manuscripts after evaluating the reviewers'

comments. Authors are invited to suggest reviewers. Reviewers' and editors' comments should be submitted with manuscripts previously rejected by other journals.

Publication and Reprint Charges. Papers published in the *Proceedings* are subject to page charges at $35.00 per page. No free reprints are given. Charges for reprints are:

Number of Pages	1-4	5-8	9-12	13-16
Price - first 100	$30.00	$50.00	$70.00	$90.00
Extra 100	$15.00	$20.00	$25.00	$30.00

Occasionally, the Society assists authors who would otherwise pay these charges from personal funds. Inquiries should be directed to the President.

1995 ANNUAL MEETING

The **Entomological Society of Ontario** is grateful for the support received for the **Annual General Meeting** held in Ottawa on 22-24 September 1995 from: Agriculture and Agri-Food Canada.

ENTOMOLOGICAL SOCIETY OF ONTARIO

The Society, founded in 1863, is the second oldest Entomological Society in North America and among the nine oldest, existing entomological societies in the world. It serves as an association of persons interested in entomology and is dedicated to the furtherance of the science by holding meetings and publication of the **Proceedings**. The **Proceedings** publishes only fully refereed scientific papers, has a world-wide circulation, and is covered by all major abstracting and indexing services. The **Society** headquarters are at the University of Guelph. The **Society's** library is housed in the McLaughlin Library of the University and is available to all members.

An annual fee of $25 provides membership in the **Society**, the right to publish in the **Proceedings**, and receive the **Newsletter** and the **Proceedings of the Entomological Society of Ontario**. An annual fee of $10 for students provides the same rights with the exception of receipt of the **Proceedings of the Entomological Society of Ontario**. Amateur and retired entomologists can join free of charge but do not receive the **Proceedings**.

A World Wide Web home page for the **Society** is currently under construction. The URL for this home page is: http://www.utoronto.ca/forest/eso/eso.htm

APPLICATION FOR MEMBERSHIP

Name: _____

Address: _____

_____

Postal Code: _____

Please send cheque or money order to:

D.B. Lyons, Secretary
Entomological Society of Ontario
Natural Resources Canada
Canadian Forest Service
P.O. Box 490
SAULT STE. MARIE, Ontario, Canada P6A 5M7

NOTICE TO CONTRIBUTORS

Please refer to Volume 126 (1995), pages 115-117 for instructions to authors. Copies of those instructions are available from the Editor.

Vouchers are important. Authors are urged to deposit voucher material at recognized institutions to document their research and to cite the place(s) of deposit in their publications.

Note: Please provide figures to fit page sizes of the ***Proceedings****.*

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